Enamel hypoplasia in modern and archaeological caprine populations: The development and application of a new methodological approach

By

Bethan R. Upex

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Department of Archaeology

University of Durham

Abstract

Bethan R. Upex

TITLE: **Enamel hypoplasia in modern and archaeological caprine populations: The development and application of a new methodological approach.**

Archaeological research into domestic animals has demonstrated that enamel hypoplasia is a potentially valuable tool for investigating a range of archaeological topics including domestication and animal management strategies. However, research into archaeological domestic populations has been hindered by the difficulty of recording and interpreting enamel hypoplasia in high-crowned species such as caprines and cattle.

This research develops a methodological approach for recording enamel hypoplasia in high-crowned species which is applied to modern and archaeological caprine populations from three geographically distinct regions (Orkney, Kenya and Iceland). Modern caprines with known life histories are used to investigate baseline factors such as the impact of the environment and nutrition on the frequency and severity of enamel hypoplasia in caprines. These baselines are then used to interpret enamel hypoplasia in archaeological populations.

Results indicate that enamel hypoplasia frequency and severity can be linked to variation in the climate /environment as well as nutrition levels in caprine populations. By comparing enamel hypoplasia frequency and severity between populations with similar baseline factors, variation in animal management strategies can be identified. Physiological and seasonal stress events including birth, weaning, and seasonal periods of malnutrition are also identified using enamel hypoplasia in both modern and archaeological populations.

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Declaration: No material contained within this thesis has been previously submitted for a degree in this or any other institution.

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1 Introduction

1.1 General introduction to the study

Dental defects have been used in many archaeological, anthropological and zoological studies to interpret aspects of diet and general health in populations (for example: Sarnat and Schour, 1941; 1942; Goodman, et al. 1988; Moggi-Cecchi & Crovella, 1991; Guatelli-Steinberg & Lukacs, 1998; Ervynck & Dobney, 1999; Dobney & Ervynck, 1998; 2000; Guatelli-Steinberg & Skinner, 2000; Guatelli-Steinberg, 2000; 2001; Ervynck, et al. 2001; Dobney, et al. 2002; 2004; King, et al. 2005; Halcrow & Tayles, 2008; Oyamada, et al. 2008). Of the various forms of enamel defect that can occur, enamel hypoplasia can be simply defined as a deficiency in the thickness of the dental enamel, commonly resulting from physiological perturbation (stress) impacting on the ameloblasts (enamel producing cells) during the period of enamel secretion (Goodman & Rose, 1990: 59).

Dental enamel is a useful source of information about past populations health and lifestyle which, unlike bone and other biological tissues, is not subject to remodelling or degradation (Rensberger, 1997). This means that any defects occurring in the development of the tooth are locked in as a permanent record of developmental stress. The chronological process of crown formation in teeth, starting at the uppermost tip of the tooth crown and developing downwards towards the root in overlapping layers, or sleeves, provides a clear chronological sequence in the development of the enamel (Goodman & Rose, 1990; Hillson, 1986). As well as providing a permanent record of developmental stress, these incremental structures,

in the enamel provide a clear chronological framework of tooth crown growth and development (Dobney & Ervynck, 2000; Goodman & Rose, 1990).

Previous studies into enamel hypoplasia have focused on humans (e.g. Sweeney, et al. 1966; 1969; 1971; Goodman, et al. 1984; Starling & Stock, 2007; Slaus, 2008), primates (eg Guatelli-Steinberg, 2000; 2001; Guatelli-Steinberg & Lukacs, 1998; Guatelli-Steinberg & Skinner, 2000; Moggi-Cecchi & Crovella, 1991; Newell, 2003) and other species with bunodont (low-crowned) dentition such as pigs (Dobney & Ervynck, 1998, 2000; Dobney, et al. 2002; 2004; Ervynck & Dobney, 1999; Ervynck, et al. 2001). Most previous studies into enamel hypoplasia have avoided focusing on high-crowned species such as caprines due to a variety of problems including: 1) the rate of enamel attrition and its rapid removal of the upper portions of the tooth crown; 2) the length of the tooth crown causing most of the tooth to be obscured by mandibular bone; and 3) coronal cementum covering the enamel surface and potentially obscuring dental defects. The most serious of these problems is potentially the first, as dental wear not only removes the occlusal portion of the tooth and any enamel hypoplasia located in this area, it also means that there are no complete unworn tooth crowns available in caprine populations, making it difficult to link enamel hypoplasia into a chronology of dental development.

While there has been extensive research carried out into the application of enamel hypoplasia studies to archaeological human populations (discussed in detail in Chapter 3), limited research been undertaken on the potential zoo-archaeological application of enamel hypoplasia (Dobney & Ervynck, 1998). The first studies into the zoo-archaeological applications of enamel hypoplasia in pig populations (Dobney & Ervynck, 1998, 2000; Dobney, et al. 2002; 2004; Ervynck & Dobney, 1999; Ervynck, et al. 2001) revealed potential to shed light on a range of zoo-archaeological issues, such as domestication, animal management and foddering practises, as well as demonstrating the potential of enamel hypoplasia to investigate population stress factors such as birth, weaning, seasonality, diet and environmental/climatic change. However, the problems associated with the study of

enamel hypoplasia in high-crowned species, and the fact that low-crowned species such as pigs commonly make up just a small percentage of the total faunal remains recovered from archaeological sites, has limited the application of enamel hypoplasia studies in zoo-archaeological contexts.

Although there is clear potential for enamel hypoplasia to be used in a wide range of zoo-archaeological contexts, it is currently limited by the difficulties with recording and interpreting enamel hypoplasia in high-crowned species. This research attempts to bridge this gap by developing a methodology which can be applied to the recording and interpretation of dental enamel defects in high-crowned species. While this study focuses on caprines, the methodology developed can be potentially applied to other high-crowned species such as cattle. Caprines were chosen as the focus for this study as they occur commonly on archaeological sites and have reduced levels of coronal cementum compared to other common high-crowned species such as cattle and horses. By applying this methodology to modern caprine populations, this study attempts to investigate possible baseline causative factors in enamel hypoplasia formation in caprines. These are then applied to archaeological caprine populations in order to investigate the potential of enamel hypoplasia to explore various aspects of animal health and husbandry in the past. Modern and archaeological caprine populations were selected from three geographically distinct regions (Orkney, Kenya and Iceland: See Figure 1.1). Within each of these regions there were specific environmental, climatic and husbandry regimes potentially impacting on the formation of enamel hypoplasia. By selecting samples from such varied regions, a wide range of potential causative factors could be investigated, as well as allowing the methodology to be tested on a range of domestic varieties from very different areas.

Figure 1.1: Showing the location of the three geographic regions where samples have been collected.

1.2 Key research themes and questions

Three key research themes were identified, each of which investigates an aspect of the development and application of a methodology for recording, analysing and interpreting enamel hypoplasia in modern and archaeological caprine populations.

1) Methodological approaches to recording and interpreting enamel hypoplasia in caprines.
2) Understanding general stress levels, baseline causative factors and their implications for the interpretation of animal management.
3) Understanding seasonal and physiological impacts.

Within each research theme a number of key research questions are addressed. These focus on a range of issues that are fundamental to developing and understanding the potential application of enamel hypoplasia to archaeological caprine populations.

1.2.1 Methodological approaches to recording and interpreting enamel hypoplasia in caprines

Several key questions, regarding the practical application of the methodology and the interpretative issues faced when analysing enamel hypoplasia in caprine populations, are explored:

- Is it possible to develop a methodological approach that will overcome the problems associated with high-crowned species and allow enamel hypoplasia to be recorded in caprine populations?
    - *How practical is this methodology?*

- *What problems are faced in recording the data using this methodology?*

- Can a developmental chronology for caprine teeth and dental enamel be created?
    - *What are the problems associated with the development of dental chronologies in caprines?*
- Are there any problems with the interpretation of the data using this methodology?

1.2.2 Understanding general stress levels, baseline causative factors and their implications for the interpretation of animal management.

Several key questions are addressed, exploring the potential of enamel hypoplasia to investigate 'physiological stress' and its interpretation in caprine populations.

- Does enamel hypoplasia reflect 'general stress' at a population level in caprines?
- What are the underlying factors that affect enamel hypoplasia in caprine populations?
    - *Does climatic and environmental variation impact on enamel hypoplasia formation in caprines?*
    - *Does nutrition impact on enamel hypoplasia formation in caprines?*
- Can variation or change in animal management strategies be seen in the enamel hypoplasia of caprine populations?
    - *How can enamel hypoplasia be used to identify animal husbandry practises?*

1.2.3 Understanding seasonal and physiological impact in caprines.

Two key research questions regarding the identification of specific physiological and seasonal events which lead to the formation of enamel hypoplasia in caprine populations are further explored:

- Are physiological stress events such as birth and weaning, visible in the enamel hypoplasia record for caprine populations?
    - *Is the nutritional and physiological stress of birth visible in the enamel hypoplasia record?*
    - *Is the nutritional and physiological stress of weaning visible in the enamel hypoplasia record?*
    - *Are any other physiological stress events such as gestation and lactation identifiable in the enamel hypoplasia record?*
- Are seasonal environmental / nutritional stress events visible in the enamel hypoplasia record?

1.3 Outline of the study

Chapter 2 provides a detailed discussion on enamel development and structure, essential to understanding the formation and context of enamel hypoplasia. Chapter 3 reviews the extensive literature on enamel hypoplasia, looking at the definition and classification of enamel defects, their aetiology and their various uses in archaeological, anthropological and zoological contexts. Chapter 4 discusses in detail the development of the methodology used in this study, its links to other methodological approaches and some of the problems faced when investigating enamel hypoplasia in high-crowned species such as caprines. Chapter 4 also deals with the more detailed methodological aspects of the study including the use of histology to investigate crown formation rates and the results and implications of the histological analysis of caprine teeth on the recording and analysis of enamel hypoplasia.

The following 3 chapters (Chapters 5, 6 and 7) deal with specific geographic case studies of enamel hypoplasia. These three case studies apply the methodology developed in Chapter 4 to modern and archaeological populations, investigating various aspects of the research themes outlined above. Chapter 5 investigates two large modern populations from Orkney, and a small archaeological assemblage from the site of Skara Brae, Orkney. This chapter focuses on the investigation of the baseline aetiological factors of diet and nutrition in the formation of enamel hypoplasia. It goes on to investigate the identification and application of 'general stress' levels between populations for studying animal management strategies. Finally, the potential for enamel hypoplasia to investigate seasonality in caprine populations and the interpretation of enamel hypoplasia defect types and severities are investigated.

Chapter 6 focuses on modern and archaeological populations from Kenya. This chapter continues to investigate enamel hypoplasia as a general indicator of

population level stress and focuses on the baseline factors of environmental / climatic variation. This chapter develops the idea that enamel hypoplasia can be used to investigate variation in animal management strategies in archaeological populations and carries out a detailed study into Neolithic Kenyan sites (comparing both cultural groups and types of sites) using the modern population as a comparison. This chapter continues to investigate seasonality in caprine populations by looking at the seasonal impact of drought and also investigates differences between the occurrence and severity of enamel hypoplasia between sheep and goat populations.

In Chapter 7 the baseline hypotheses (preliminarily developed in Chapters 5 and 6) regarding the impact of climatic, environmental and nutritional variation on the formation and severity of enamel hypoplasia, are tested in two purely archaeological populations from Norse Iceland. This chapter investigates the practical application of enamel hypoplasia to archaeological populations and the potential for animal management strategies to be investigated from variation in the frequency and severity of enamel hypoplasia. The chapter goes on to study the impact of climate change and seasonality on enamel hypoplasia formation and severity and demonstrates the potential of enamel hypoplasia to be used in purely archaeological populations to reveal information regarding animal management strategies. Chapter 8 summarises the results of the previous four chapters in the context of the research themes previously outlined. This chapter addresses each research theme and key question in turn, providing a summary of the relevant data and results obtained. The final chapter (Chapter 9) provides a conclusion of the research results and finishes with suggestions for future work.

2 Tooth formation and development

Dental enamel hypoplasia is intrinsically linked to the underlying development and structure of teeth. It is therefore essential that some of these complex processes are discussed, providing the necessary background for the work carried out in this thesis. This chapter provides a general introduction to the physical structure and properties of teeth and their supporting tissues, as well as discussing the development of dental tissues and their internal structures. A basic understanding of the processes of dental development in all mammals is provided, although the majority of the information derives from human studies. A more specific discussion of caprine dental development is provided in the following chapter.

2.1 Teeth and their physical structure

While teeth have a variety of functions in mammals, including attack, defence and communication, their main function is mastication (Nanci, 2008). This requires them to be hard wearing, durable and able to withstand the high levels of force created during this process. In most mammals, the teeth are attached directly into the jawbone providing a firm, yet brittle structure. This means that teeth are often lost or broken during the course of normal function (Nanci, 2008). As teeth, once formed, cannot be altered in size or shape, a limited succession of teeth occurs in most mammals. However, this is not normally to compensate for the loss or damage of teeth but is due to the large increase in size which occurs with the growth and development of juvenile mammals. The smaller jaws of juveniles can only carry a limited number of small (deciduous or primary) teeth and as the animal grows, these become inadequate and are subsequently are replaced by a higher number of larger (secondary or permanent) teeth (Nanci, 2008).

Teeth consist of two main elements, the root and the crown (Hillson, 2005; Goodman & Rose, 1990). The crown, under normal conditions is the part of the tooth which protrudes into the mouth and is used in mastication. The root is the part of the tooth that sits in the jawbone below the gum line and anchors the tooth into the mouth. These two parts of the teeth (the root and the crown) are constructed from three different dental tissues; the enamel, dentine and cementum, with each playing a key role in the function and use of the tooth (Figure 2.1).

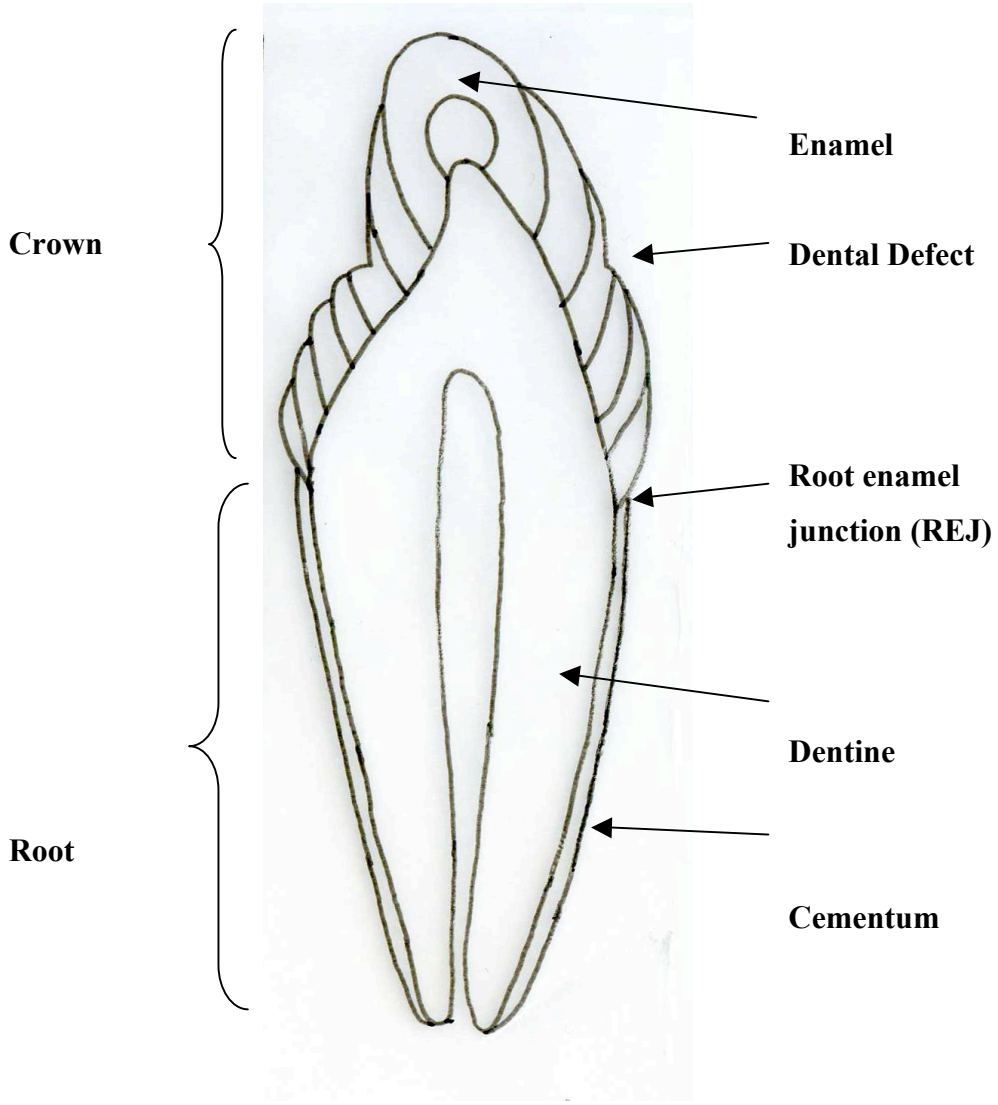

Figure 2.1: Showing the various parts and structures of a tooth (After Goodman & Rose, 1990: 63, Figure 1).

2.1.1 Organic and inorganic composition of teeth

All three of the dental tissues which make up teeth are mixtures of mineral and organic components. The inorganic component consists almost entirely of calcium phosphate minerals in the form of apatite (Fincham, et al. 1990; Nanci, 2008). Apatite is a family of minerals composed of phosphate (PO_4^{2-}) and calcium (Ca^{2+}) ions, its general formula is $Ca_{10}(PO_4)_6X_2$. X can be one of several different ions but the most commonly occurring are hydroxyl (OH^-) and fluorine (F^-). The apatite crystallises into long narrow crystals which are approximately hexagonal in cross section, reflecting the internal structure of the crystals (Hillson, 1996; 2005).

The main organic component of dental tissue is collagen. This is a compound constructed from 20 different amino acids with high levels of glycine, proline and hydroxyproline which is unique to collagen (Williams & Elliott, 1989). In each molecule of collagen, the amino acids join together to form chains which then spiral around each other forming fibrils between 10 – 100 nm in diameter. Apatite crystals are then seeded into gaps between the fibrils. In addition to the minerals and collagen there is a small amount of organic material in the dental tissues, including various peptides, lipids and glycoproteins (Fincham, et al. 1990;Hillson 2005).

2.1.2 Enamel

Enamel is the hard, protective, mineralised outer layer of the tooth (Goodman & Rose, 1990). Enamel varies in colour from white / grey to yellow and is, in normal conditions, translucent. Its colour is influenced by its thickness, in areas where it is thin, the yellow dentine shows through. Enamel varies greatly in thickness over the different parts of the tooth, being thinnest at the cervical line and thickest on the occlusal surfaces, where in humans it can be up to 2.5 mm thick (Nanci, 2008). Enamel covers the more sensitive dentine and pulp cavity and protects them from bacterial attack and decay. When mature, enamel is unique amongst mammal tissues. It is almost entirely inorganic in content, with 96-97% of its weight being made up of

mineral elements (Williams & Elliott, 1989; Goodman & Rose, 1990; Maas & Dumont, 1990; Fincham, et al. 1990). The remaining components of enamel consist of 3.6-2.1 % water, and a very small percentage (0.4 – 0.9 %) of organic material (Scott & Symons, 1974). This makes enamel the hardest tissue in the human body and comparable with mild steel, varying between 5 and 8 on the Mohs scale (diamond being 10). This makes it ideally suited to the mechanical and chemical stresses it encounters in the oral environment (Nanci, 2008).

The mineral component of enamel consists of crystalline mineral salts, composed almost entirely of hydroxyapatite (crystalline calcium phosphate, Fincham, et al. 1990). Each of these crystallites is at least 1600nm long, making them longer than bone and dentine crystallites (Hillson, 1996; 2005). These crystallites are arrayed with their long axes running parallel to each other and are packed closely together to form a fine, dense crystalline mass. Within this structure the crystallites form enamel rods or prisms which are interspersed with inter-rod or aprismatic enamel (see Figure 2.2). It is between these inter-rod and rod regions, trapped in gaps between the crystals, that the small organic components of enamel can be found (Fincham, et al. 1990). The structure of these rod and inter-rod regions is highly complex and it is this internal structure, combined with the high degree of mineralisation, which allows enamel to withstand the high levels of masticatory force and the constant attack from acid, from food and bacteria that are found in the mouth (Nanci, 2008).

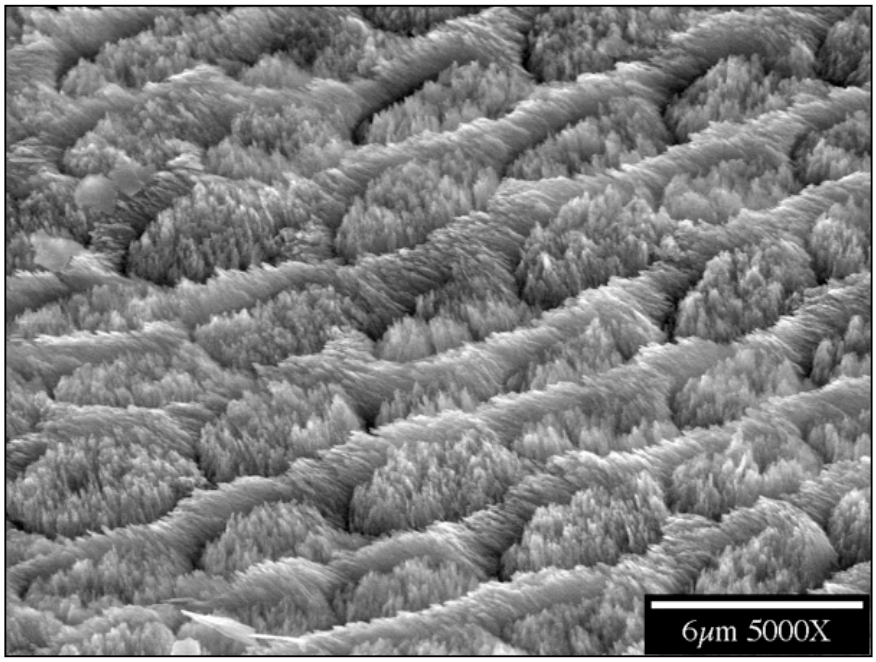

Figure 2.2: SEM of etched enamel showing enamel crystallites forming rod and inter-rod enamel (http://www.sdm.buffalo.edu/scic/gallery.html).

2.1.3 Dentine and pulp

Dentine is the more flexible and resilient layer which lies under and supports the enamel. Like enamel, dentine is also a mineralised tissue, and the mineral component of dentine is also apatite. However, dentine has a much lower mineral content than enamel and a much higher organic component (Bosshardt & Selvig, 1997). The high mineral content and the complex crystalline structure of enamel make it very hard but also very brittle, and without the support of the dentine it would fracture under the crushing forces produced during mastication (Hillson, 1996; 2005; Nanci, 2008).

Histologically, one of the key features of dentine is the closely packed tubules that run through its entire thickness (Bosshardt & Selvig, 1997; Nanci, 2008, Figure 2.3). These tubules contain the cytoplasmic extensions of the odontoblasts cells which

initially excreted the dentine. These cells, unlike the ameloblasts that secrete enamel, are not lost during the course of dental eruption or throughout the life of the individual (Hillson, 2005). They stay within the tooth forming the peripheral boundary between the dental pulp and the edge of the dentine and subsequently can secrete more dentine as and when needed. This makes dentine a sensitive tissue that is able to remodel and repair itself (Bosshardt & Selvig, 1997).

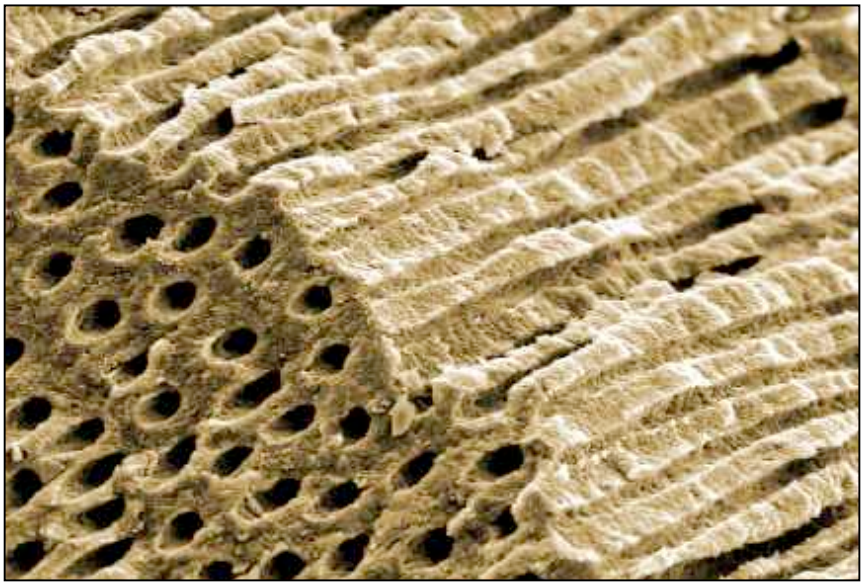

Figure 2.3: Thin section though human dentine

(From: http://www.cmeba.univrennes1.fr/Applications_sciences_vie.html).

The final structure found in any tooth is the pulp chamber. This is located in the very centre of the tooth and contains living tissues, with a nervous and blood supply connected to the rest of the body through the root of the tooth. Functionally dentine and pulp are inseparable. The pulp has several roles but all revolve around nourishing and protecting the cells which secrete the dentine (Nanci, 2008).

2.1.4 Cementum and periodontal ligaments

In mammals, the roots of teeth are anchored into the surrounding alveolar bone of the jaw by the cementum and the periodontal ligament. These provide the teeth with a

firm yet flexible attachment, enabling them to withstand the powerful forces produced in mastication. In high-crowned species, the cementum also develops over the enamel surface providing a firm attachment for the teeth during the long period of crown development that occurs in these species. In low-crowned species, the enamel surface is protected from the development of cementum before tooth eruption by the presence of the ameloblasts (H. Kierdorf, pers. Comm.). These cells, once they have secreted and matured the enamel, switch into a protective role, covering the newly formed enamel until it erupts into the mouth.

The mineralised component of cementum is again apatite, with collagen forming the majority of the organic element. Cementum can be either acellular or cellular, the second type produced when the cells which secrete the cementum (cementocytes) become trapped in their own matrix and form lacunae within the cementum. The cementum provides a firm anchorage for one end of the periodontal ligament, with the other end embedded in the alveolar bone (Hillson, 1996; 2005). The periodontal ligament is a highly specialised connective tissue and able to adapt to the shifting pressures and forces of mastication. Each bundle of fibres is like a spliced rope in that individual collagen strands are able to remodel without altering the overall structure or integrity of the ligament (Nanci, 2008). This allows the ligament to adapt to the direction and strength of the applied forces without compromising the attachment of the tooth. The other important role of the ligament is sensory. As enamel is an inert tissue it is the periodontal ligament which helps (along with other senses) mammals to identify when their teeth are in contact with each other (Nanci, 2008).

2.2 Early stages of tooth development

The surfaces of an embryo's mouth are lined with a layer of tissue known as the epithylium and below this, a layer of cells called the mesenchyme. These tissues will ultimately develop into the many different types of tissue which make up the jaws and lower face. The teeth are sequentially formed by the interactions of ectodermal and mesenchymal tissues, through a series of developmental phases. In humans, after approximately 37 days of development, two bands of epithelial cells have formed over two arches composed of the mesenchymal cells. These two arches correspond to roughly the location of the upper and lower jaws (Hillson, 1996). The epithelial cells quickly differentiate, forming the dental and vestibular lamina. In sheep the dental laminar is apparent approximately 33 days after conception and like most mammals this forms a continuous band along the line of the jaw (Witter & Míšek, 1999). On the anterior aspect of the dental lamina, continued cell activity produces a series of epithelial outgrowths. By the tenth week in humans, there are ten of these outgrowths on each dental arch and these will eventually form the deciduous dentition.

2.2.1 Bud and cap stages

The beginning of the 'bud' stage is marked by the incurrence of the epithelial outgrowths into the ectomesenchyme of the jaw. These cells form the tooth buds that will ultimately develop into the teeth (Figure 2.4). The buds are surrounded by closely-packed supporting ectomesenchymal cells (Nanci, 2008). As the bud grows and expands, the ectomesenchymal cells condense at the base of the bud producing an area with a high density of cells, known as the dental papilla. This will ultimately form the dentine and the pulp of the tooth. The mesenchymal cells around the outside of the bud form a bag-like structure around it; this is known as the dental follicle (Nanci, 2008). The dental follicle will ultimately form the cementum and the bud will become the enamel. In the 'cap' stage the enamel organ has expanded to the point where it sits over a ball of ectomesenchymal cells and the dental papilla like a cap. Towards the end of the cap stage, the enamel organ begins to differentiate, producing the inner enamel epithelium. It is this layer of cell that will eventually

form the enamel matrix (Nanci 2008). In sheep the dental cap for the first permanent molar appears at approximately 39 days after conception and this changes into the bell stage of dental development at around 51 days after conception. The tooth bud of the second molar appears around 53 days after conception (Witter & Míšek, 1999).

2.2.2 Bell stage

The last stage of early development is the 'bell' stage, so called because the continued growth of the enamel organ leads to a deepening in the underside of the cap, producing a bell-like shape (see Figure 2.5). It is towards the end of the bell stage that the inner enamel epithelium begins to take on the shape of the dentine enamel junction (DEJ), making the structure of the future crown recognisable (Nanci, 2008). The cells of the inner enamel epithelium and messenchyme begin to undergo a series of differentiations, becoming ameloblasts and odontoblasts. They align themselves so that they are facing each other; this border will eventually form the DEJ. The cells then begin to secrete enamel and dentine and work backwards away from each other in a process known as amelogenesis. Also, in this stage of development, the tooth is eventually separated from the oral epithelium as the dental laminar breaks down (Nanci, 2008).

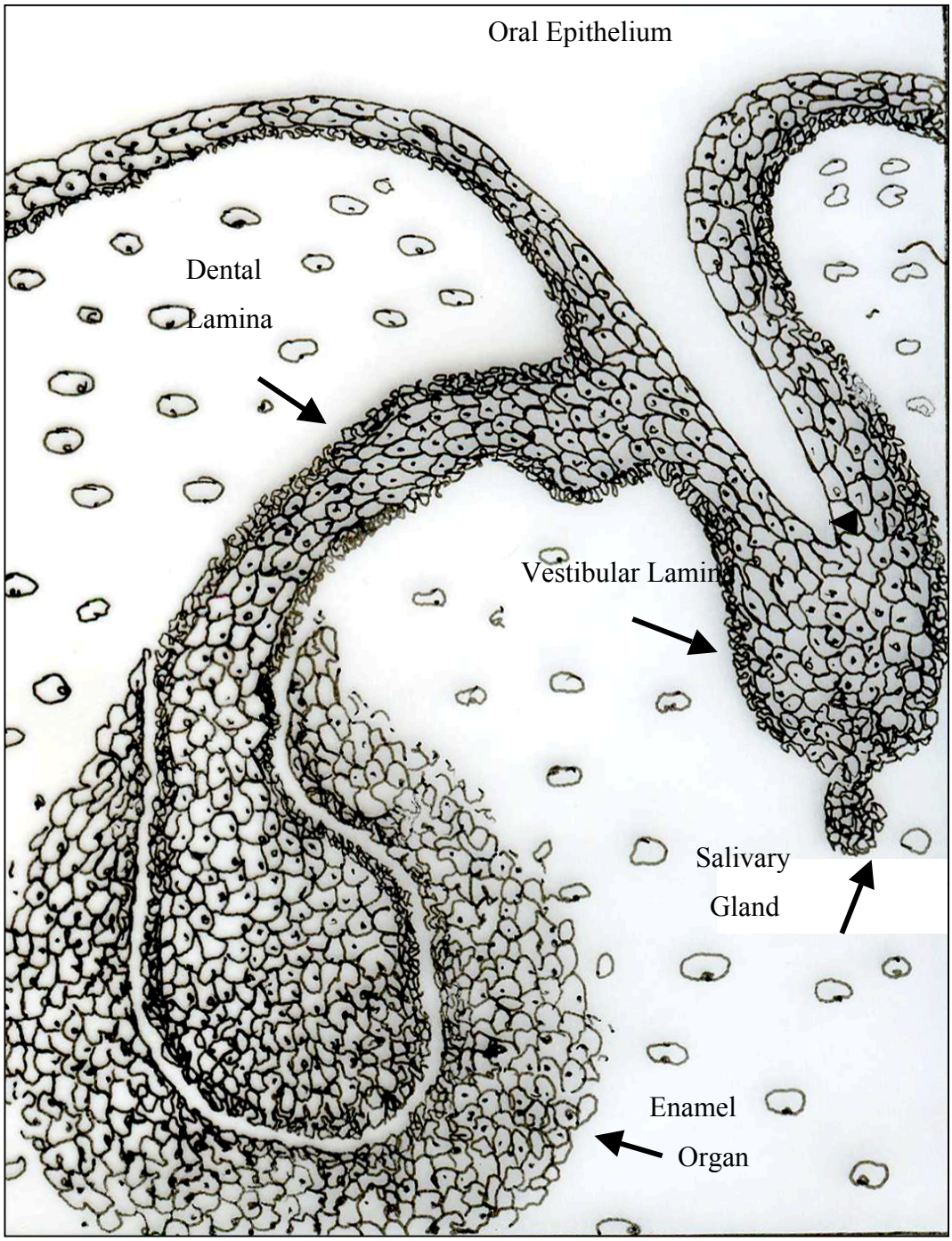

Figure 2.4: Showing the bud stage of dental development. An epithelial bud (enamel organ) has formed at the end of the dental lamina which extends out from the oral epithelium. At the bottom of the vestibular lamina is the initial epithelial proliferation leading to the formation of accessory salivary glands (From Philipson & Reichart, 2004: Figure 1).

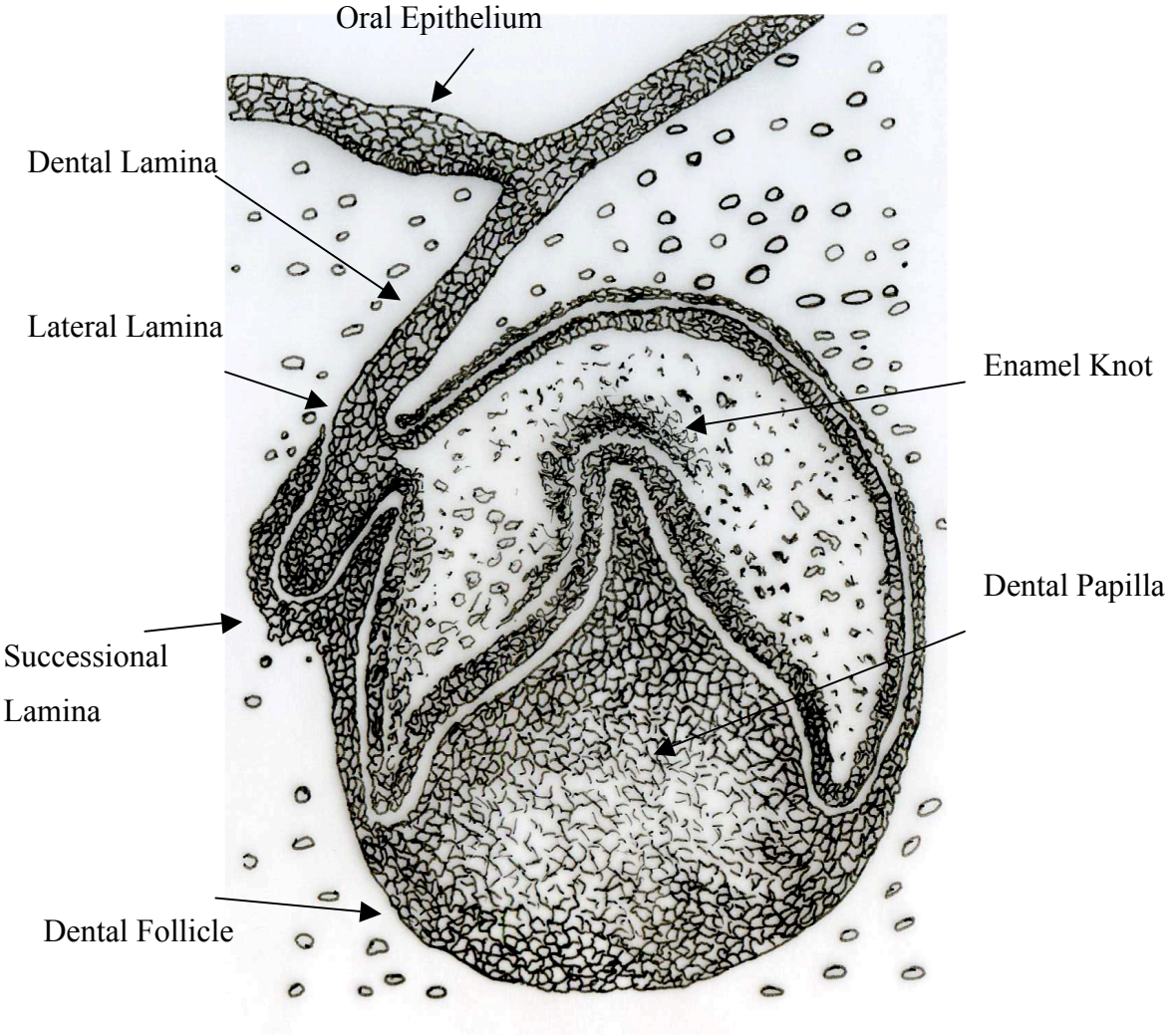

Figure 2.5: Showing the bell stage of formation for a deciduous tooth germ. The tooth germ occurs on the labial aspect of the dental lamina extending from the oral epithelium. An epithelial bridge (the lateral lamina) connects the dental lamina with the bell-shaped tooth germ. The free tip of the dental lamina proliferates into the ectomesenchyme as the successional lamina, providing the anlage for a permanent tooth. The enamel knot sits on top of the dental papilla which will ultimately form the dentine and pulp. The dental follicle surrounds the bud and will form the cementum (From Philipson & Reichart, 2004: Figure 2).

2.3 Enamel formation and structure

2.3.1 Amelogenesis

Both enamel and dentine are formed in layers or sheets, produced by two separate groups of cells. Enamel is formed by epithelial cells (ameloblasts) and dentine from mesenchymal cells (odontoblasts). The ameloblasts are long, narrow, highly polarised, cylindrical cells which are packed closely together forming a sheet, with each cell having one end in contact with the developing enamel front (Hillson, 2005). Amelogenesis is the process by which enamel is formed and can be divided into three phases; pre-secretory, secretory and maturation. In the first phase, the ameloblasts prepare to secrete the enamel matrix; in the second the cells produce the organic enamel matrix and organise the entire thickness of the enamel and in the final stage the cells transport ions, removing the organic component and mineralising the enamel matrix. Each ameloblast is involved in all stages of enamel production and maturation, over its own distinct territory (one rod and its surrounding inter-rod enamel), for the full thickness of the tooth (Nanci, 2008).

Enamel, deposition begins at the very tip of the tooth cusp and is deposited in overlying domes. Once the full height of the enamel at the occlusal surface is complete, the ameloblasts then move down the surface of the tooth depositing enamel in sleeves until the crown is complete. Dentine is secreted in the same way, with both secretion fronts slowly moving away from each other secreting tissue until the tooth is complete. The odontoblasts begin the process by secreting the initial dentine layer at the tip of the tooth. The ameloblasts then follow by secreting the initial aprismatic enamel layer against the newly formed dentine. This boundary, however, is not distinct as the first hydroxyapatite crystals formed interdigitate with the dentine, locking the tissues together (Nanci, 2008). For around 300 days (in humans) the ameloblasts are committed to secreting the amelogenin, they then switch to maturing the enamel. The secreted matrix consists of many of the structures present in mature enamel, though with a higher organic content (approximately 30% of its weight), and is a complex mixture of enamel proteins, water, citrate, and lipids with crystallites seeded within it. It is basically a growing medium for the enamel

crystallites; maturation removes many of the organic components and allows the crystallites to fully develop (Saski, et al. 1997).

As the layer of ameloblasts moves away from the enamel dentine border (at an angle to the long axis of the cell) the secreted matrix (amelogenin) is seeded with crystals. These orientate themselves away from what will become the centre of the enamel rod. The formation of the enamel rods is closely linked to the presence of the Tomes process, named after the 19th century Swedish anatomist C. S. Tomes who first identified these structures. It is this part of the cell which is responsible for the secretion of the enamel matrix and ultimately for the unique structure of the mature enamel. In the early stages of secretion only the proximal portion of the Tomes process is present. However, in the later stages it develops a distal portion that projects into the enamel matrix (Hillson, 1996; 2005; Nanci, 2008). As secretion gives way to maturation the ameloblasts reduce in size until they are 50% of their original height and the Tomes process disappears and is replaced by a 'ruffled' cell wall. This is assumed to be associated with the removal of the amelogenin and water and the formation of the apatite crystals. This ruffled end is modulated with a smooth end and this transformation appears to occur in waves which move along the developing crown surface from the most immature regions of enamel to the most mature regions of the enamel. The ruffle ended cells allow inorganic material to be incorporated into the enamel and the smooth ends permit organic material and water to move out of the enamel (Nanci, 2008) During this period the seeded crystallites expand rapidly both in width and thickness and develop into the structures found in mature enamel.

2.3.2 Rod and inter-rod enamel

Mammalian enamel is composed of two fundamental units or types: rods and inter-rod enamel (Figure 2.6). In human teeth there are approximately 12 million enamel rods, formed by an equal number of ameloblasts (Osborn & TenCate, 1983). These rods are formed by the enamel crystallites being organised into bundles between 4 and 12 μm wide. The formation of these two types of enamel is very closely linked to the form taken by the end of the ameleoblast during the secretion phase. In the first

few days of enamel matrix production, the ameloblasts have a flat end (the proximal Tomes process) in contact with the developing enamel front, producing a layer of aprismatic enamel. After the initial aprismatic layer of enamel has been formed then the distal Tomes process develops (Hillson, 2005).

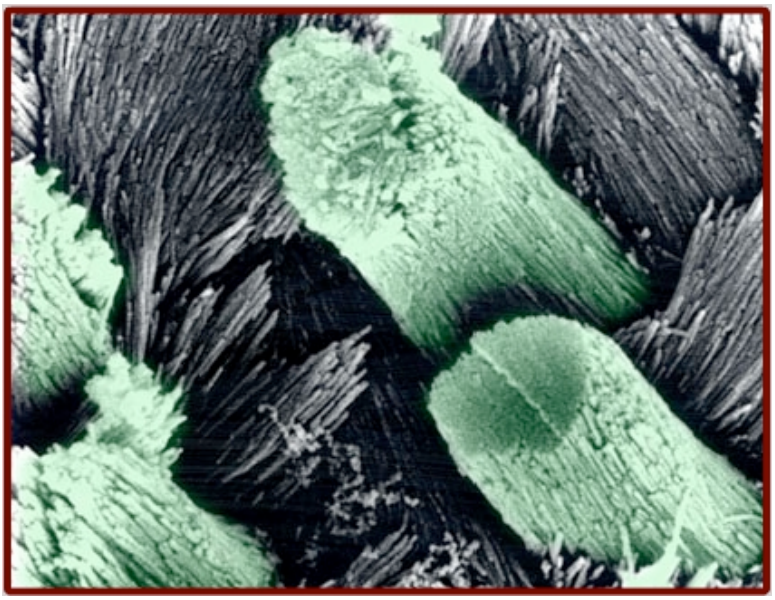

Figure 2.6: Showing enamel rods (green) and inter-rod enamel.

From: http://dentistry.uic.edu/CraniofacialGenetics/ResearchTED.htm.

The distal process extends into the enamel matrix and secretion continues from both the distal and proximal Tomes processes. Enamel secreted from the distal process forms rods, with the enamel secreted from the proximal process forming inter-rod enamel. At both sites, the enamel produced is identical in its composition and the only difference between the two is the orientation of the crystallites. Formation of the inter-rod enamel is always a step ahead of the formation of the rod enamel, as the inter-rod enamel defines the pit into which the rod enamel is secreted by the distal Tomes process (Nanci, 2008). If the ameloblasts are removed from the enamel in this phase then the Tomes process pits can be seen on the surface of the enamel (Figure 2.7). When these are present on the surface of a completed tooth, it indicates that development stopped quickly as under normal circumstances a layer of aprismatic

enamel is laid down on the surface of the tooth. Subsequently the enamel of a tooth is composed of three layers sandwiched together, a thin initial aprismatic layer, a rod containing layer, and another thin aprismatic final layer. As the initial, inter-rod and final enamel layers are all secreted from the same part of the cell (proximal Tomes process) it is assumed that they form a continuum.

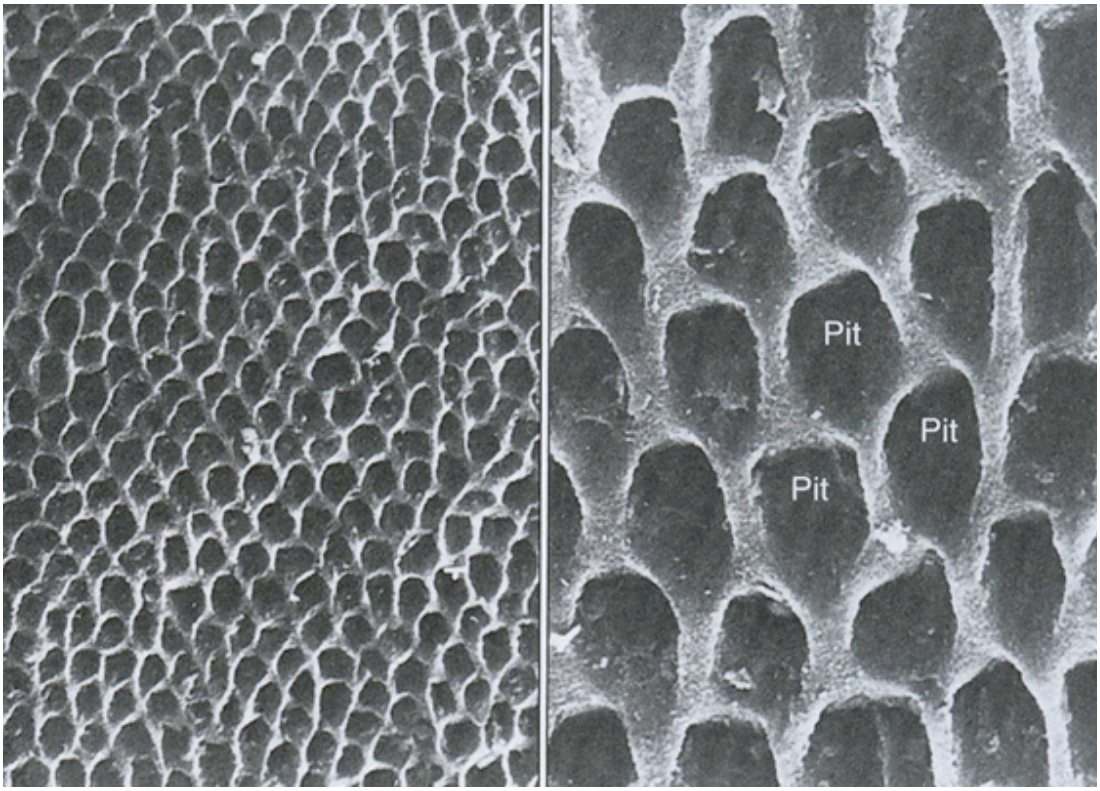

Figure 2.7: SEM of a developing human tooth with the ameloblasts removed. The surface shows a series of pits which were originally filled with the distal Tomes processes, the pit walls are formed from inter-rod enamel (From Warshawsky, et al. 1981: 396).

The boundaries of the enamel rods are formed by discontinuities in the direction of the enamel crystals produced by the presence of the Tomes process, and it is in the gaps produced at these boundaries where most of the organic components of enamel are found. However, there are variations within these boundaries which produce three different patterns of rod structure (Figure 2.8). The first of these patterns is when each rod possesses a complete cylindrical rod boundary. Each rod sits in a complete tunnel of inter rod enamel. The second pattern is where the prisms are

arranged into vertical rows and are horseshoe-shaped, having incomplete cylindrical boundaries. The rods are separated by inter-row sheets of aprismatic enamel. The final pattern also produces incomplete, horseshoe-shaped rods and the prisms are again arranged in rows, but this time in a vertical matrix. The inter-rod enamel is attached as a 'tail' to the enamel rod and sits between the two enamel rods below it. All three of these enamel patterns are normally found in most teeth. However, different groups of mammals tend to show a preference to one pattern. For example the third pattern is common in primates (Hillson, 2005).

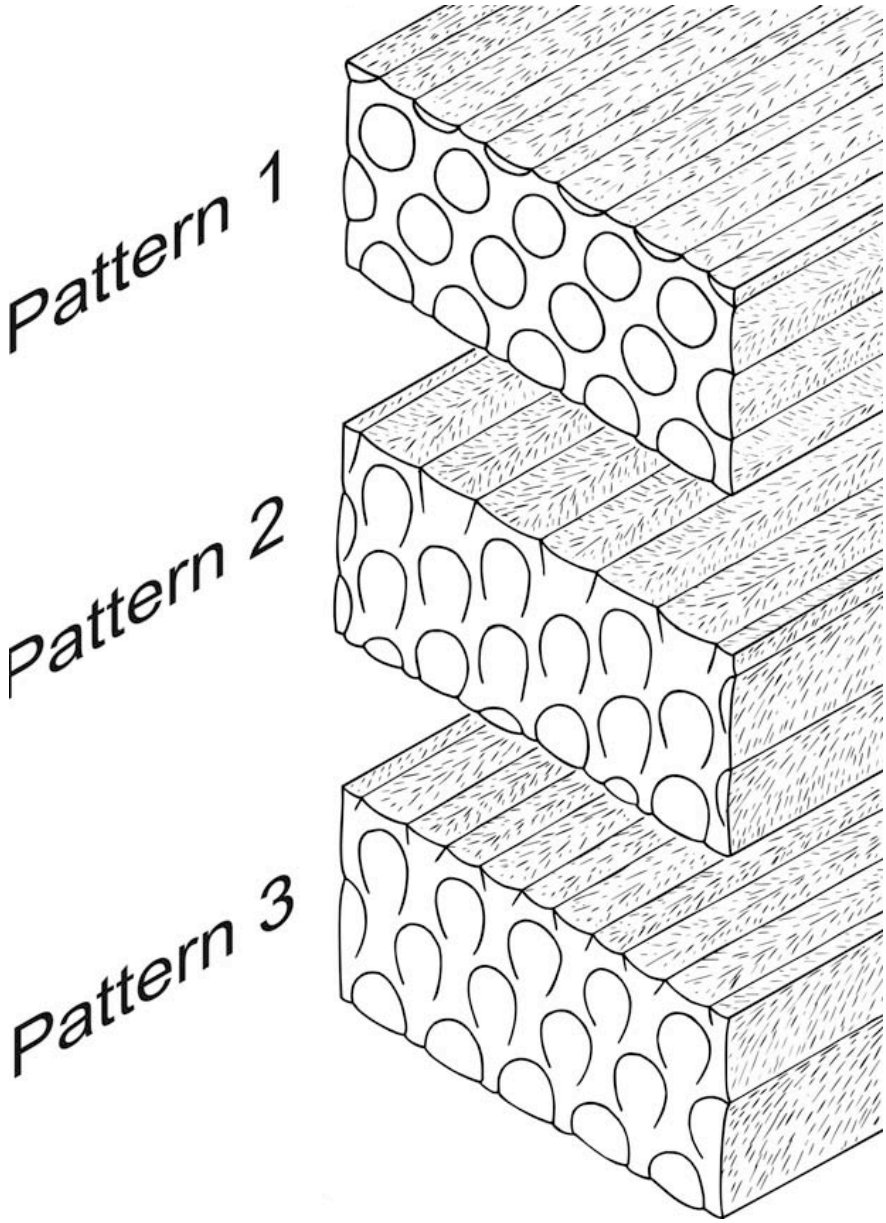

Figure 2.8: Patterns of enamel structure (From Hillson, 2005, figure 2.2 pg 157).

2.3.3 Hunter-Schreger Bands

In only very few mammals do the enamel rods run in a straight course from the dentine enamel junction to the tooth surface. In the majority of mammals the rods follow a sinuous course, known as 'enamel decussation'. This is caused by the complex movements of the ameloblasts during the secretory phase of enamel production (Hillson, 2005). Neighbouring prisms run a very similar course but slightly out of sequence, producing a wave-like form that runs down the tooth surface (Figure 2.9).

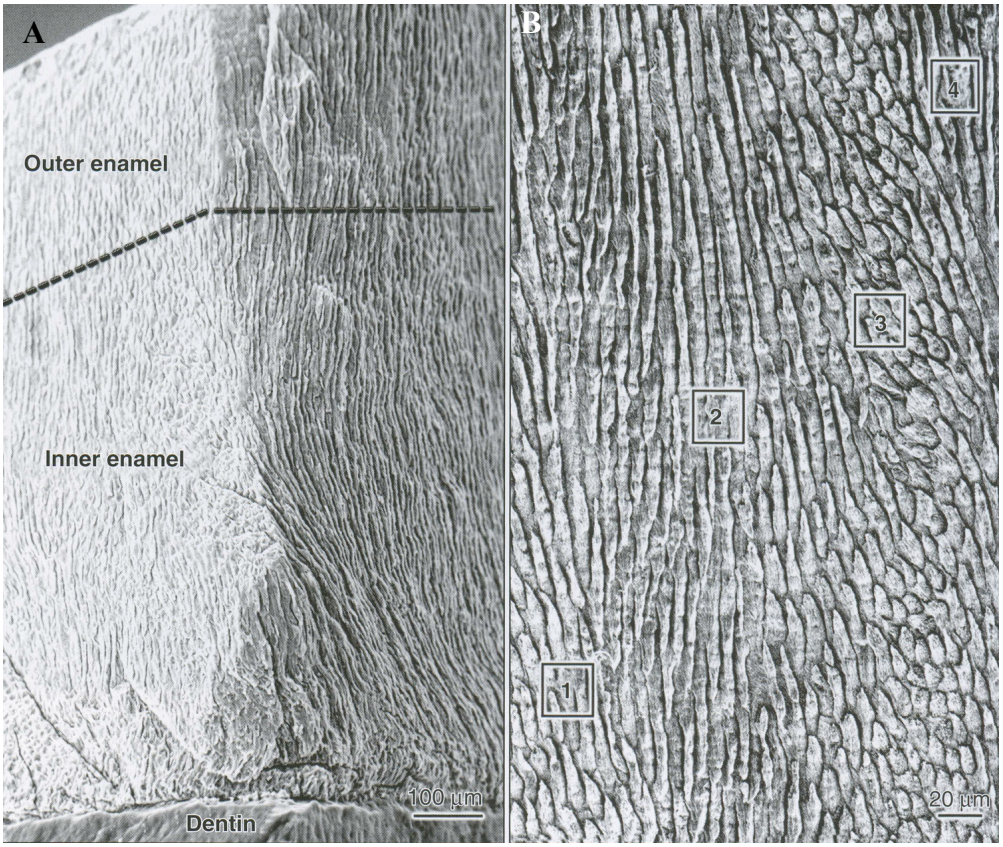

Figure 2.9: Showing: A) the complex sinusoidal trajectory of enamel prisms. B) The 4 resulting different orientations of rods when sectioned, leading to the formation of Hunter Schreger bands (From Nanci, 2008: 168)

This sinusoidal form produced by the enamel, causes alternating bands of light and dark zones, referred to respectively as parazones and diazones. In the parazones the rods are sectioned longitudinally so their crystallites have their long axes parallel to

the plane of the section making them appear as bright areas. In the diazones the crystallites are sectioned obliquely and show up as darker areas (Figure 2.10). The pattern produced by these parazones and diazones are known as Hunter-Schreger bands and they can be seen radiating out from the dentine-enamel junction for about two thirds of the enamel thickness. In the final third of the enamel (closest to the surface) the enamel rods are too tightly packed for the bands to be visible (Nanci, 2008).

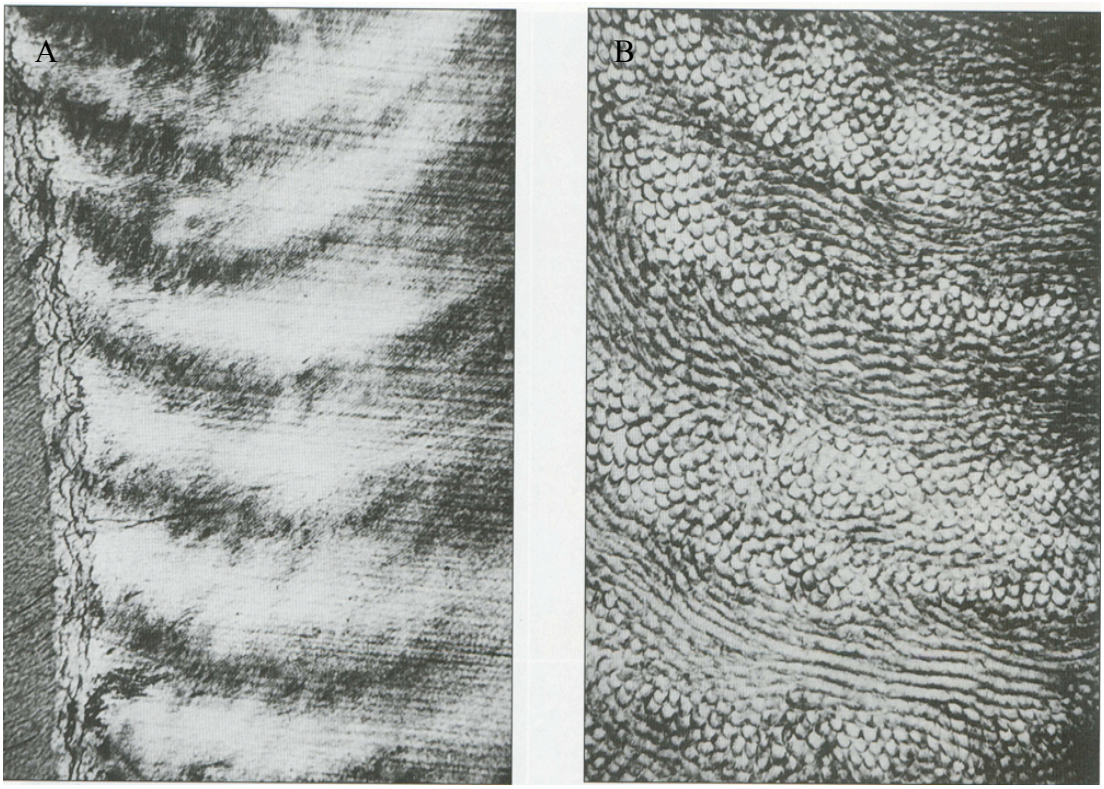

Figure 2.10: Showing: Hunter Schreger bands (A) produced when a section cuts though prisms in both oblique and longitudinal zones (B) (From Nanci, 2008: 183).

2.4 Incremental enamel structures

Generally, enamel rods run in a perpendicular direction towards the dentine. Near the tip of the crown they tend to run at a vertical angle to the dentine enamel junction, with this angle becoming more obtuse nearer the cervical portion of the tooth. On top of this pattern there are two other important incremental patterns that occur within the enamel structure.

2.4.1 Cross striations

These striations appear in ground sections of enamel as bands of light and dark alternating along the length of the rod and appear to be related to differing degrees of mineralization within the rod (Schmidt & Keil, 1971; Boyde, 1979). When these striations are viewed using scanning electron microscopes, constrictions along the enamel rod are visible, relating to the location of the light and dark striations (Figure 2.11). It is thought that these patterns reveal diurnal rhythms in the ameloblasts, giving rise to periods of accelerated and decelerated matrix production. As these rhythms affect the Tomes process, variation occurs in the direction of the seeded crystallites causing a wavy edge to form along the edge of the rod. Counts of the number of cross striations from the DEJ to the enamel surface along prisms correlate well with estimates of the time taken for the crown to develop. Research undertaken on children with a known age-at-death showed a very close correlation between known age and the number of cross striations found (Boyde, 1990, 1963). As these cross striations are linked to 24hr rhythms (approximately one light and one dark band every 24hrs) they have proved a useful tool in investigating the development and timing of the crown formation in several groups of primates, including humans (e.g. Dirks, 1998; Reid, et al. 1998; Macchiarelli, et at. 2006).

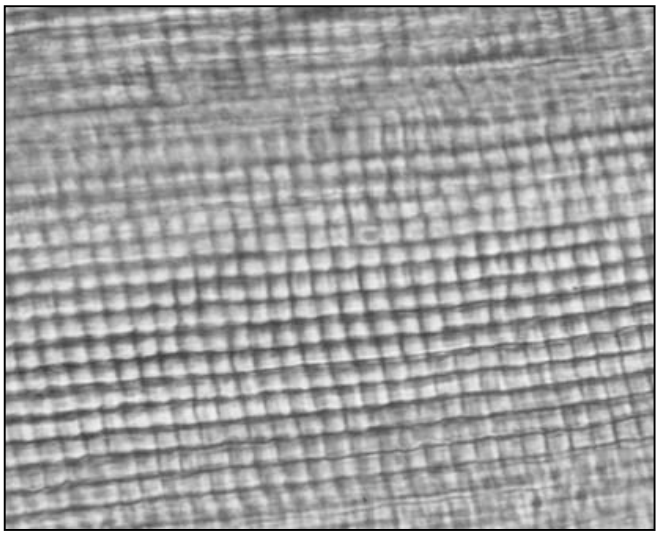

Figure 2.11: Showing a cross-section of a human second molar. The rods run almost horizontally across, broken at regular intervals by cross striations. Striae of Retzius can also be faintly seen running diagonally left to right (Hillson 2005: 160, figure 2.3).

2.4.2 Striae of Retzius

The striae of Retzius were first identified and described by Anders Retzius (1837), a Swedish anatomist. The striae of Retzius are another regular pattern that occurs in enamel and show up as brown fuzzy lines which run across the enamel prisms, from the dentine enamel junction to the tooth surface. These striae are often ascribed to a circaseptan rhythm (in humans) in enamel development which produces disruption to the structure of the enamel rod (Hillson, 1996). Striae of Retzius are very variable, both within teeth and between species. They can appear as a continuous line through the enamel or a discontinuous line and can vary in width from between 4μm up to 150μm; however, the majority of Retzius lines are narrow. The striae are also associated with a slight shift in the rods direction; this can vary from a slight notch to an obvious bend. It is on this basis that Wilson & Schroff (1970) defined two types of striae of Retzius.

Line striae: fine brown lines often more clearly visible close to the crown surface and associated with a slight bending or notching of the rods.

Band striae (or 'Wilson Band'): broad in comparison with line striae and found throughout the enamel including the cusp and deep enamel regions, and also associated with a sharp bend in the prism, normally translocating the prism in cervical direction (Hillson, 2005).

The idea that wide, brown striae may be related to pathological disturbances was first suggested by Gustafson (1959; Gustafson & Gustafson, 1967). Wilson & Schroff (1970) also defined pathological striae as bands in which rod directions made abrupt changes that were associated with 'atypical' rod forms. The extent to which these bands are truly pathological is not completely clear. However, there does appear to be a strong link between systemic disturbances and the variation found in the striae of Retzius. This is supported by the presence of the neonatal line found in enamel, first described by Schour (1936) following work by Rushton (1933). This neonatal line is an enhanced Retzius band that appears in teeth that were developing at the time of birth. The neonatal line is often quite broad (between 20-30μm wide) and shows many of the features associated with a pathological Wilson band. The enamel found below the neonatal line (pre-birth) exhibits far fewer line striae and other irregularities, possibly representing the more protected intrauterine environment. The line itself is regarded as evidence of the physiological stress caused by birth (Whittaker & Richards, 1978).

Other evidence to suggest that Retzius bands are related to systemic stress appears on the surface of the crown. Striae of Retzius outcrop on the surface of the tooth producing wave-like structures know as perikymata (Figure 2.12 and Figure 2.13). These take their name from the Greek *peri* (around) and *kymata* (waves) (Hillson & Bond 1997). In the furrows of the perikymata (the location of the striae of Retzius), rows of Tomes process pits can be found. This indicates that the ameloblasts have switched straight from enamel secretion into enamel maturation, without producing the normal layer of aprismatic enamel found over the ridge of the Perikyma.

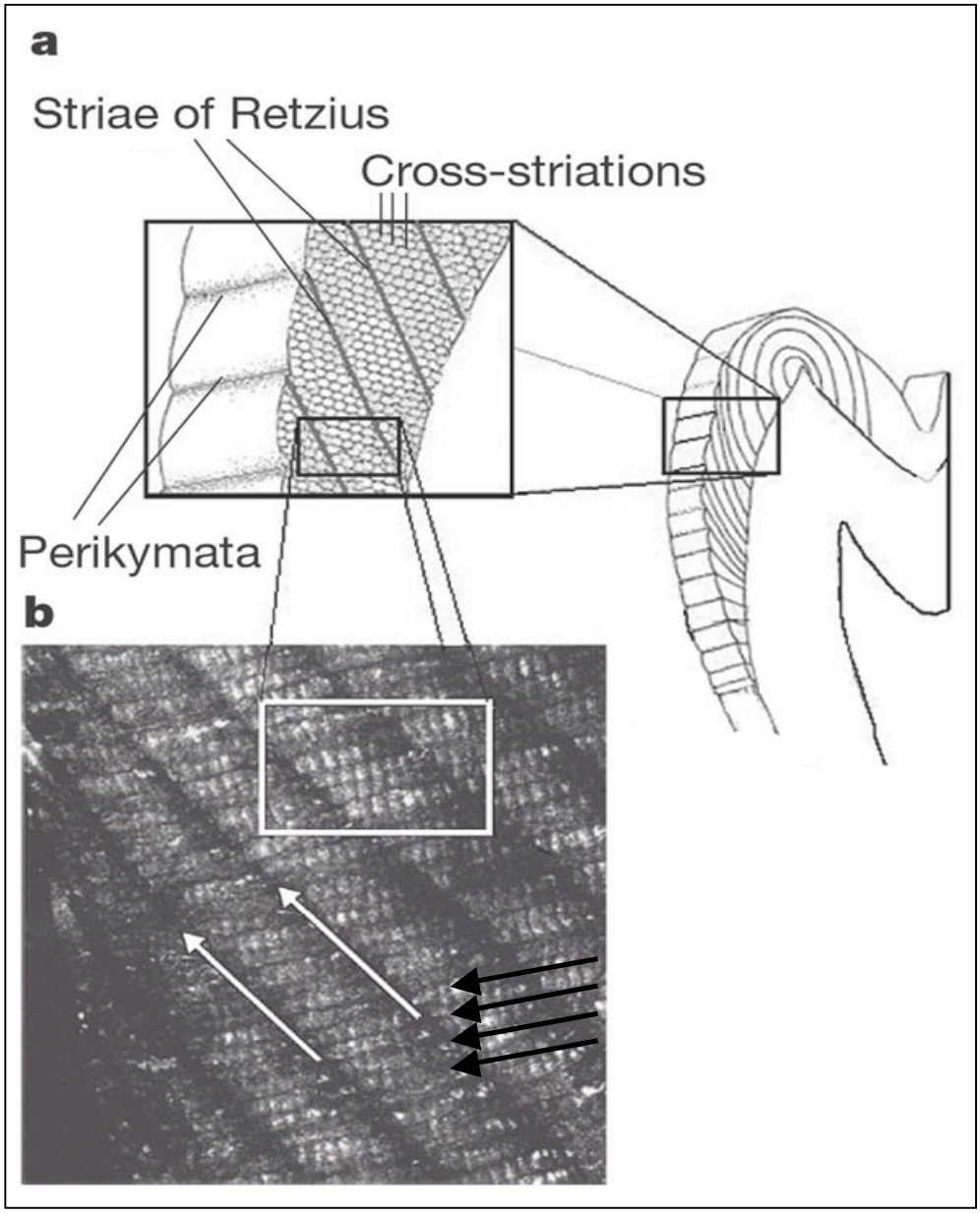

Figure 2.12: a) The relationship between the striae of Retzius and the perikymata on the tooth surface. b) A cross section though striae of Retzius. The striae are indicated by white arrows and the direction of the prisms is indicated by black arrows (After Moggi-Cecchi, 2001).

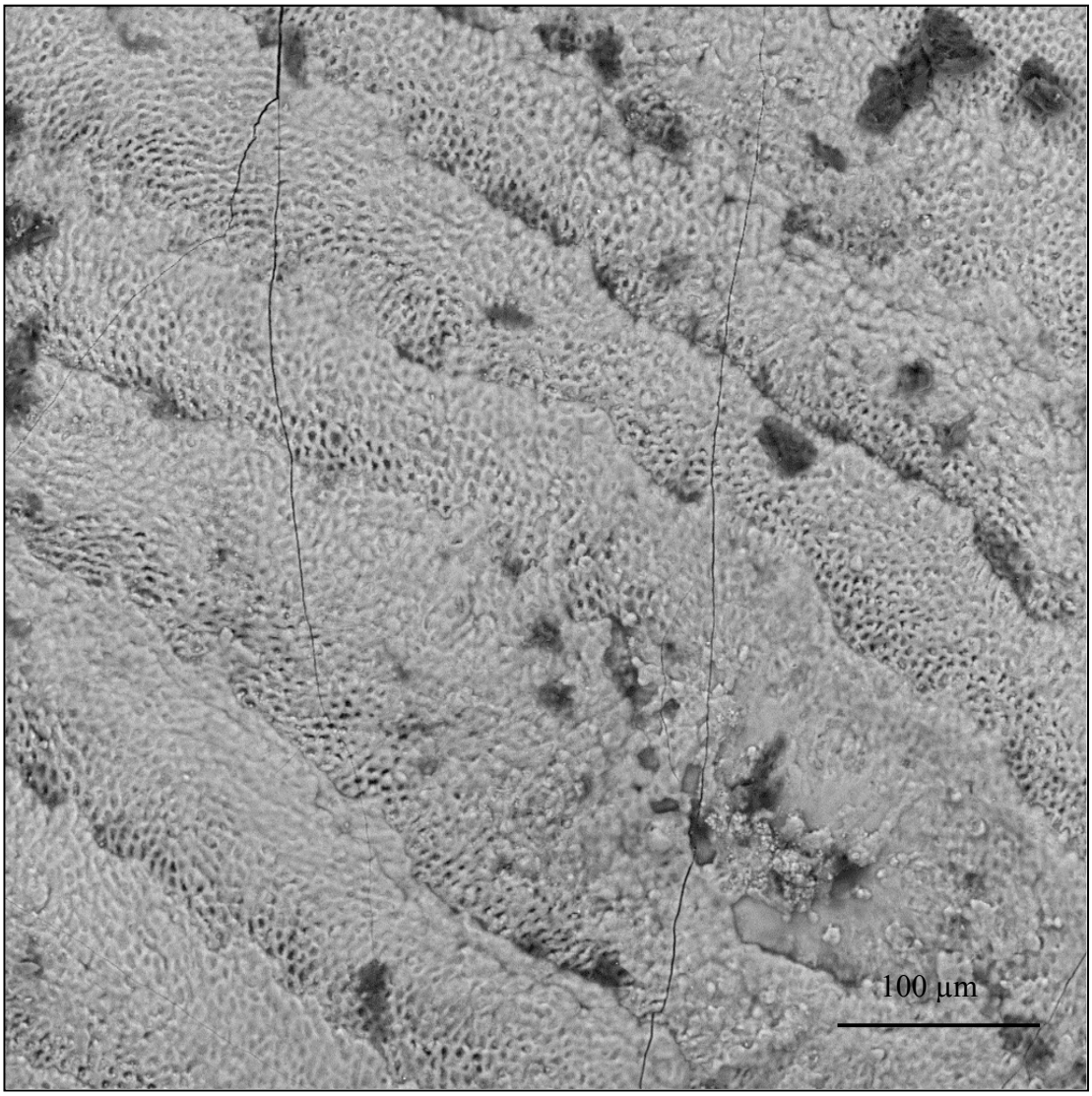

Figure 2.13: Showing the striae of Retzius outcropping on the surface of a of a caprine molar as wave-like perikymata. Tomes process pits are clearly visible in the furrows but not in the ridges. NB the image is slightly rotated. The occlusal surface is towards the upper right of the picture, the perikyma run horizontally across the tooth surface (Witzel, Unpublished).

Prominent striae (or Wilson bands) can also be matched up across the different teeth in one individual, relating to the same stress event. This and the fact that the numbers of cross striations between the pathological striae remain the same, strongly indicates that some form of systemic change during the course of development causes these

defects. Wilson bands are also often associated with enamel hypoplasia visible on the tooth surface (Goodman & Rose, 1990). These defects are known to be associated with illness, malnutrition and a variety of other stresses and their link with Wilson bands therefore also supports the idea that the striae of Retzius may be related to such underlying systemic stresses.

The striae of Retzius also represent the growth of the enamel, beginning at the tip of the tooth and building up until eventually the enamel develops in sleeves down the tooth surface. The average human molar contains approximately 120 striae of Retzius; the first 30 – 40 of these are hidden within the enamel at the tooth tip. These are called 'appositional striae' and are located at the tips of the tooth crown. Where the striae outcrop at the surface producing perikymata they are called 'imbricational striae'. As with the cross striations, the striae of Retzius have been used to calculate the length of time of tooth crown development, and in cases where the teeth were still forming, the striae have also been used to estimate the age-at-death (Boyde 1963; 1990).

2.5 Tooth structure and the formation of enamel hypoplasia

Dental enamel hypoplasia are produced in the secretory phase of amelogenesis as a consequence of ameloblast impairment due to stress. The type of stress and its duration can produce several different types of enamel defects (discussed in detail in the next chapter). But all are caused by the ameloblast cells either slowing down the secretion of enamel or stopping secretion entirely. The exact effect on the cells is dependent on a multitude of factors, including the secretory phase and age of the cells. For example in humans it has been demonstrated that secretory ameloblasts which have been active for longer periods of time are more likely to cease enamel matrix production as a result of stress, than the younger ameloblasts which are located more cervically on the developing enamel front (Witzel, et al. 2008). In this respect enamel hypoplasia are intrinsically linked to the formation and internal structure of teeth. Indeed, the most commonly occurring form of enamel hypoplasia (line type) can be seen as more prominent expression of the perikymata formed on the tooth surface where the striae of Retzius outcrop. The periodicity of the striae of Retzius and their clear link to the formation of enamel hypoplasia make enamel defects into permanent chronological markers of these stress events. The relationship between the ameloblasts and their reaction to physiological perturbations, combined with the chronological internal structure of the teeth, therefore make enamel hypoplasia a valuable tool for investigating a multitude of issues which can be identified through the study of early life stressors.

3 Literature Review

This chapter provides an outline of past and present work on enamel hypoplasia. It outlines what enamel hypoplasias are, what causes them, and provides a summary of previous key studies utilising enamel hypoplasia in both human and animal populations. Not surprisingly, many of the examples involve human studies, since this is where the majority of enamel hypoplasia research has been carried out. However, discussions of the aetiology of enamel hypoplasias in humans are relevant to other mammals like caprines featured in this PhD research.

3.1 Defining enamel hypoplasia

Dental defects have been identified in the literature from as early as 1743, when they were described as 'tooth erosion' by Frenchman Robert Bunon, who suggested that they were caused by rickets, measles and scurvy (Bunon, 1743 cited in Sarnat and Schour, 1941: 1942). In the following years, hypoplastic defects of dental enamel were described variously as 'black decay of teeth' (Sanchez, 1785 quoted in Sarnat & Schour 1941: 1989) and 'notched incisors' (Hutchinson, 1858) It was not until the end of the nineteenth century that the term 'hypoplastic enamel defect' was first used (Zsigmondy, 1893, cited in Dobney 1991). The word hypoplastic comes from the Greek (*hypo* meaning 'under' and *plastikos* meaning 'mould') and has become the most generally accepted term to describe quantitative deficiencies in dental enamel formation.

3.1.1 Definitions of dental defects

When viewed with the naked eye, the enamel of the tooth normally appears as whitish, translucent and smooth. Defects of the dental enamel are therefore, anything that affects one or more of these three features of 'normal enamel'.

Dental enamel defects can be divided into three groups:

1) Discolouration: these can be deposits of pigment which occur in the tooth due to various metabolic conditions, or the result of later staining of areas of deficiently mineralised enamel.

2) Opacities: these are areas of hypocalcified enamel and are caused by disruption of the ameloblasts in the enamel maturation stage.

3) Hypoplasia: This is one of the most commonly identified forms of enamel defect.

Enamel hypoplasia can be simply defined as deficiencies in enamel thickness, and are most commonly manifested as horizontal bands of irregular enamel, producing lines, or grooves, across the tooth surface, that are parallel with the root enamel junction (REJ). They can also be seen as individual or multiple clusters of pitting on the enamel surface (Hillson, 1996: 165).

3.1.2 Clinical definitions of dental enamel defects

Dental enamel defects, whatever form they take, are the result of disruption to the ameloblasts during matrix secretion or maturation (Suckling, 1989). There have been multiple attempts at categorising and classifying enamel defects based on their causes and forms (for example, Orban, 1957; Stones, 1966; Schultze, 1970; Pindbourg 1982; Sarnat & Moss 1985). Broadly speaking, enamel defects can be

separated into: a) disturbances which affect enamel secretion, leading to a reduction in the thickness of the enamel layer; and b) disturbances which affect the maturation of the enamel, leading to hypo-calcification or hypo-maturation of the enamel. Sarnat and Moss (1985) describe three simple categories of defect type by further separating the types of defects caused by disturbance to the maturation of the enamel.

1) Defects in quantity: hypoplasia caused by disturbance in the secretion of enamel matrix.

2) Defects in quality: hypocalcification, caused during mineralization, leading to soft / chalky enamel.

3) Defects in crystallisation: hypomaturation, caused by disturbances in the mineralization, leading to defective crystal formation and structure

Initial research suggested that disturbances which affected the secretion of enamel, produced hypoplasia type defects and disturbances that affected the maturation of the enamel produced hypomineralised and hypocalcified defects (Goodman & Rose, 1990). However, research by Suckling (1986; 1989) challenged this assumption and demonstrated that hypocalcification could also be the result of a disturbance in the secretion of the enamel matrix. Suckling's work demonstrated that while secretory cells are preferentially affected by systemic insults leading to the formation of hypoplastic defects, demarcated opacities could also be the result of a milder but longer lasting systemic insult during the secretory phase of enamel formation (Suckling: 1986; 1989).

3.1.3 Types of enamel hypoplasia

This research focuses purely on hypoplastic defects, as these are the most commonly occurring defect type. Hypoplastic defects of enamel can be further divided into several different types.

Line-type and plane-type hypoplasia

Line-type hypoplasia are the most commonly-occurring form of hypoplastic enamel defect. These defects occur in the imbricational zone of enamel and consist of narrow, clearly defined, horizontal bands running across the tooth surface (see Figure 3.1). These defects form part of a continuous sliding scale from the macro to the microscopic. In its most ephemeral form, this defect appears as only a slight exaggeration of a single or few adjacent perikyma grooves. Histological analysis of this type of defect by Witzel, et al. (2006), demonstrated that these defects were not commonly associated with underlying pathological striae of Retzius or other abnormal enamel microstructures. Instead this type of defect was related to an increase in the spacing between perikyma grooves in the occlusal wall of the defect, producing a larger exposed incremental plane. This suggests that a higher than normal number of ameloblasts had prematurely ceased secretion of dental enamel.

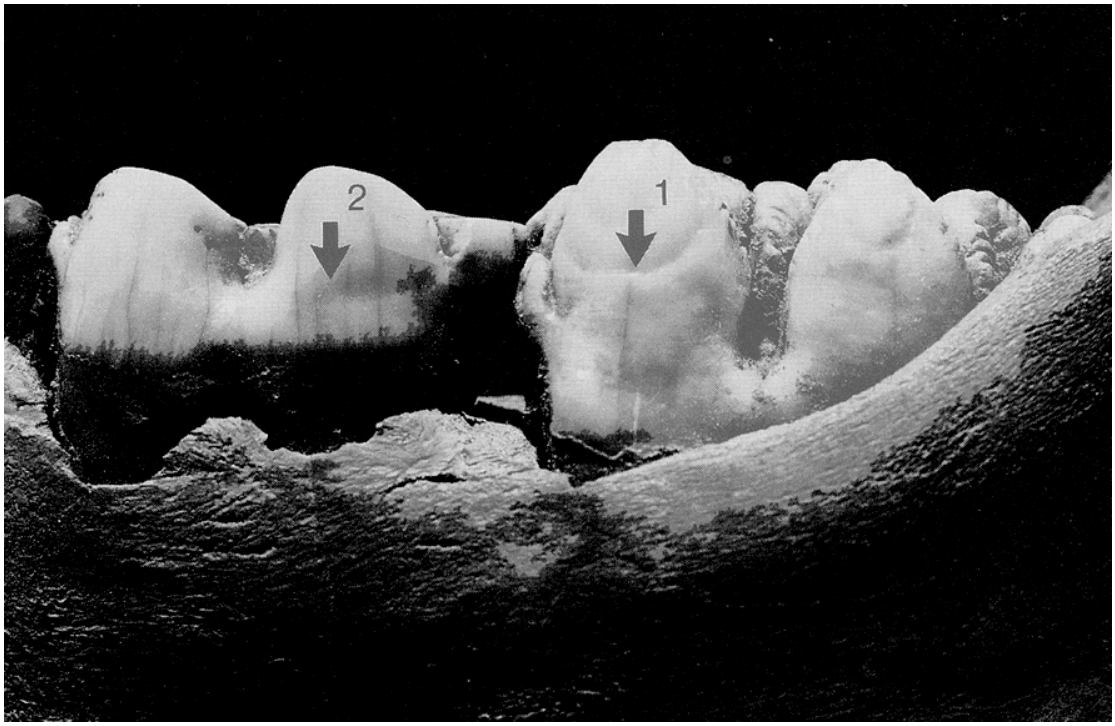

Figure 3.1: Showing enamel hypoplasia (LEH) on the second molar and third molar of a medieval domestic pig from Ename (Belgium). 1 = line-type, 2 = depression (from Dobney, Ervynck & La Ferla, 2002: Figure 1). For explanation of 'depression-type' hypoplasia, see below.

Macroscopically it can be difficult to separate line-type and plane-type hypoplasias as both form a distinct line or furrow which runs around the tooth surface, but histologically there is a clear difference (see Figure 3.2 Figure 3.2). 'Plane-types' hypoplasia are so called because the impact on the ameloblasts is so severe that they stop producing enamel completely, leaving behind an exposed incremental plane which can commonly be traced extending into the tooth as a pathological striae of Retzius (Witzel, et al. 2006). These defects produce extended areas of reduced enamel thickness and represent a more severe impact on the ameloblasts. Due to the difficulty of separating these features macroscopically, in this research all linear form defects are referred to as 'line-type' but are also scored on severity, based on the size and depth of the line. These distinctions serve to separate the low impact 'line-type' from the more severe but otherwise indistinguishable 'plane-type' defects.

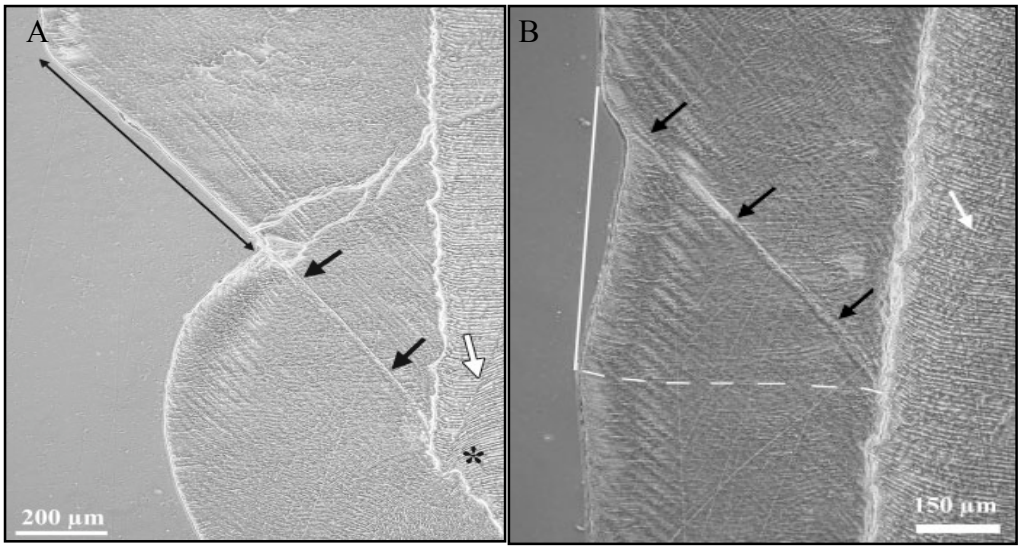

Figure 3.2: A = plane-type defect, black arrows indicating accentuated pathological striae and exposed incremental plane, white arrows showing matching striae in dentine. B = line-type defect, black arrows indicating accentuated pathological striae, solid white line showing the area of affected amelobleasts and the dashed white line showing the hypothetical path of the youngest ameloblast affected. The white arrows in both images show matching striae in dentine, (from Witzel et al. 2006)

In the case of plane-type defects the ameloblasts closest to the enamel surface are most commonly involved (Witzel, et al. 2006; Suckling & Thurley, 1984). This suggests that in humans the ameloblasts in the later stages of secretory activity are more susceptible to stress and subsequently permanently stop matrix secretion, while the ameloblasts in the early stages of secretion are more able to recover and resume matrix secretion. In its most extreme form this type of hypoplasia can result in a complete absence of dental enamel over the whole or part of the tooth.

Pit-type

Pit-type defects can vary greatly in size and in number. They can be arranged in small clusters or in bands running across the tooth surface parallel with the perikymata, often with an accompanying line-type defect (see Figure 3.3). Single large pits are also common and have often been associated with isolated traumas,

although recent studies have suggested that isolated pit hypoplasia could also be due to systemic stress (Franz-Odendaal, 2004).

Figure 3.3: Showing pit defects on the surface of a caprine first molar (Witzel unpublished).

Pit-type defects are formed by the same processes that produce line-type defects but, unlike line-type defects where all the cells are uniformly affected, pits are formed when only small clusters of cells cease matrix production, while their neighbouring cells are able to continue enamel secretion. The fact that many pits are located in furrows or depressions indicates that all the ameloblasts are affected to some extent, but the underlying reasons for the variation found between neighbouring cells remains unknown (Witzel, et al. 2006).

Depressions

Depressions were first identified as a possible pathological defect by Dobney and Ervynck (1998). Work by Witzel, et al. (2006) demonstrated that depressions in pig

teeth were the result of a clear concavity in the dentine enamel junction and a reduction in the thickness of the enamel. Both of these factors combine to produce a clear depression in the surface to the tooth (see Figure 3.1 above). Histologically the enamel underlying depressions appears normal, except for slightly accentuated incremental markings and a reduction in the spacing of the striae of Retzius, indicating a slowing down in the rate of enamel secretion over an extended period of time (Witzel, et al. 2006). This suggests that depressions are caused by sustained periods of low level systemic stress, where the stress is not severe enough to cause a complete reduction in the distal portion of the Tomes process, just a slowing in the rate of enamel secretion. For example, Dobney and Ervynck (1998) suggest a prolonged period of nutritional stress in pigs during the winter months as a cause for the depression-type hypoplasias identified in their research.

3.2 Aetiology

There have been multiple attempts to classify hypoplasia purely on the basis of specific aetiological factors (Orban, 1957; Stones, 1966; Schltze, 1970; Sarnat & Moss, 1985). Due to the diverse nature of hypoplastic defects, and the wide range of conditions which lead to their formation, many of these definitions are unusable. Of all of these definitions it has been Orban's (1957) that is perhaps the most applicable, and can be used to provide reliable preliminary classifications of dental defects (Dobney, 1991). These definitions allow hypoplasia to be reliably diagnosed as resulting from one of three causal conditions: hereditary anomalies; systemic or metabolic disturbances and localised trauma (Shawashy & Yaeger, 1986; Suckling, 1989; Weinman, et al. 1945).

Hereditary anomalies**:** These defects generally affect all teeth equally and affect both the primary and secondary dentitions. The defects affect either the dentine or the enamel but rarely both as is commonly found in systemic anomalies. The defects are also normally very severe and bear no relationship to a particular period in crown development (Weinman, et al. 1945; Gorlin & Goldman, 1970; Stewart & Poole, 1982).

Systemic disturbances: These defects are found on any teeth that were developing at the time of the disturbance and are subsequently found in a variety of different positions on the tooth crown, relating to the level of tooth development when the disturbance occurred, producing a symmetry between defects on both sides of the teeth and the dental arch (Weinman, et al. 1945; Shawashy & Yaeger, 1986).

Localised trauma: Defects caused by local trauma are nearly always isolated events. They lack the symmetry of the systemic defects and often take the form of large isolated pits or areas of missing enamel. As with hereditary defects, localised trauma

can produce quite severe dental defects (Weinman, et al. 1945; Andreasen, et al. 1971; Ravn, 1975; Skinner & Hung, 1989).

3.2.1 Hereditary anomalies

Dental defects can be inherited on their own or as a symptom / condition of a wider disease. Defects which arise from hereditary anomalies are commonly known as 'Amelogenesis Imperfecta'. These defects are produced by the failure of the enamel to develop, either partially or completely, and can be divided into several sub-classes (Sundell & Valentine, 1986). There is only one known archaeological example of ameleogenesis amperfecta described by Cook (1980). In archaeological populations, individuals with hereditary dental defects are quite rare, as most hereditary conditions which cause dental defects often produce other congenital problems making long term survival uncommon (Pindborg, 1970). It is for this reason that hereditary dental defects in domestic animals are almost never seen, as animals with congenital diseases are rarely allowed to survive and reproduce within managed herds of economically important species. Subsequently hereditary defects are afforded little space here as the most common forms of hypoplasia in livestock species are those caused by systemic or metabolic stresses.

3.2.2 Systemic disturbances

Systemic disturbances can be further divided into those deriving from malnutrition, disease and toxicity.

<u>Malnutrition</u>

Malnutrition is a broad term, covering a wide range of vitamin, protein and mineral deficiencies. Adequate nutrition is a vital factor in the growth and development of young mammals as malnutrition can disrupt and potentially even completely suspend physiological growth and development. Malnutrition also weakens the immune system, making malnourished individuals susceptible to a whole host of

opportunistic infections and disorders. There have been a wide range of epidemiological studies in human populations, investigating links between malnutrition and enamel hypoplasia. For example, Goodman, et al. (1987) investigated the frequency and chronology of hypoplasia occurrence in five rural communities in Mexico, in each of these communities there was endemic mild to moderate malnutrition. Forty six percent of all the children included in their study had enamel hypoplasia. Sweeney, et al. (1966) also found a clear association between the degree of malnutrition suffered by children and the number of hypoplastic defects occurring on the deciduous upper central incisors in Guatemalan children. Their research compared two groups of children - one group with second degree malnutrition, the other with third degree malnutrition. Forty three percent of the children with second degree malnutrition showed hypoplastic enamel defects compared to the 73% of children with third degree malnutrition. Similar work was carried out by Rugg-Gunn, et al. (1998) in malnourished Saudi children, investigating the variables behind their malnourished status and their relationship to enamel hypoplasia formation. They linked malnourishment to economic status, and also noted increased levels of enamel hypoplasia occurrence in malnourished children.

Studies by Goodman, et al. (1988; 1989a; 1989b) clearly demonstrated the role of malnutrition in the formation of enamel hypoplasia. Goodman, et al. (1988; 1989a; 1989b) looked at a sample of children from Mexico where half had been given nutritional supplements since birth and half had not. The half without nutritional supplements showed nearly twice the frequency of linear enamel hypoplasia compared to the supplemented individuals. The relationship between malnutrition and increased prevalence of enamel hypoplasia was also demonstrated by Zhou and Corruccini (1998) in their study of individuals who lived through the 1959 – 1961 Chinese famine. Individuals who had had teeth developing during this famine showed higher levels of enamel defects than those who had not. They also noted an increase in enamel hypoplasia frequency in individuals who lived in rural locations versus those who lived in urban locations and related this to poorer standards of living and malnutrition in rural populations.

There has been a wide variety of experimental work carried out looking at the specific roles of certain vitamin and mineral deficiencies in animals. Some of the earliest experiments were carried out on Beagles who were fed a range of vitamin D, calcium and phosphorus deficient diets, producing a variety of clearly demarcated enamel hypoplasias (Mellanby, 1929). Other vitamins such as Vitamin A & C have also been extensively studied. Vitamin A is an essential vitamin for the maintenance of the epithelial tissue in the body. As differentiation of the enamel organ is essential for normal tooth development to proceed and the enamel organ is comprised of epithelial tissues, there has been considerable research carried out into the impact of this vitamin on amelogenesis (Jontell & Linde, 1986). Baume, et al. (1972) demonstrated that vitamin A deficiency caused foetal rats to begin odontogenesis at least two days later than control rats with normal levels of vitamin A. Mellanby (1941) investigated vitamin A deficiency in rats was able to demonstrate that the severity of the hypoplasia produced in new born rats was directly related to the duration of vitamin A deficiency in the mother. Pindborg (1970) identified only one known case of vitamin C deficiency leading to hypoplasia formation in humans. However, in animals, vitamin C deficiencies have been demonstrated to have a wide range of effects on tooth enamel (Zilva & Wells, 1919; Wolbach & Bessey, 1942; Berkovitz, 1974; Messer, 1972). Vitamin C is essential for the hydroxylation of protein during collagen synthesis and deficiencies in vitamin C can cause serious defects in the formation of collagen (Jontell & Linde, 1986).

Some of the most important animal research has been carried out in sheep by Suckling, et al. (1983; 1986) where 34 sheep were infected with varying numbers of nematode parasites during the development period of the central permanent incisor. The sheep were given varying doses of the parasite, with the infections being treated and cured between a) 7 and 10 days after infestation in the high dose animals and b) approximately 54 days in the moderate to low dose animals. These animals were then compared to 14 control sheep from the same breed that had been left uninfected.

Parasitic infection causes anorexia, local mal-absorption and alterations in the mineral metabolism, effectively producing severe malnutrition in the affected

animals. The infected sheep which received high doses of the parasite showed severe systemic effects including anorexia, lassitude, scouring and weight loss; the moderate and low dose animals showed less severe signs of infection, producing a more chronic low level systemic insult. Twenty two percent of the animals developed enamel hypoplasia, totalling 9 animals, 8 of which were animals in the high parasitic infection group.

While it is considered relatively easy to identify and separate linear enamel hypoplasia from other hereditary or traumatic enamel defects, the causes of enamel hypoplasia remain non-specific. Cutress and Suckling (1982) suggest that there are over one hundred factors which may produce hypoplastic enamel defects. Subsequently hypoplasia is not the perfect marker for nutritional stress due to the wide variety of other causes (Goodman & Rose, 1991). However, the modern epidemiological studies do clearly demonstrate a positive correlation between malnourishment and dental enamel hypoplasia formation and they suggest that even quite small changes in nutritional status can produce large differences in the frequency of enamel hypoplasia.

Disease

As previously mentioned, the earliest reference to enamel hypoplasia suggests it is related to measles, rickets and scurvy (Bunon, 1743, cited in Sarnat & Schour, 1941: 1942), and it was not until 1785 that other medical conditions such as syphilis were first reported in relation to dental defects. Hutchinson (1858) was the first to describe the specific forms of dental defects that characterise congenital syphilis, and other early writers link hypoplasia formation to rickets or to a combination of both syphilis and rickets as the primary aetiological factors (Gottlieb, 1920).

The idea that hypoplastic enamel defects could be related to a particular systemic incidence has been investigated numerous times. There have been a wide range of studies focusing on specific aetiological causes of enamel hypoplasia. Lindermann

(1958) focused on gastrointestinal diseases. He studied 141 Danish children with non-specific episodes of diarrhoea. Of these 141 children, 22%, showed hypoplastic defects in their permanent teeth and in 31% of these individuals he was able to correlate their episodes of diarrhoea with enamel hypoplasia formation. In a Swedish study, Grahnen and Selander (1954) found that hypoplastic enamel defects were present in 25% of all patients studied who had rickets during childhood, compared with just 3% who had hypoplastic defects in their control group. Rattner & Meyers (1962) demonstrated that enamel defects occur in 58% of children with congenital allergies. Jackson (1961) reported a correlation between the occurrence of hypoplasia and individuals who had exanthematous fevers before the age of three. This finding was disputed by Willson & Cleaton-Jones (1978), who demonstrated in a separate study that 18 of the 30 children they studied who had had exanthematous fevers, showed no correlation between the age at which the illness had occurred and the position of enamel defects on their teeth. Finally, Ortega Paez, et al. (2008) investigated children with coeliac disease and found that 83% showed enamel defects compared with 53% of children without the condition.

Sarnat and Schour (1941; 1942) were the first to attempt to relate known pathological conditions from individuals with known life histories to hypoplasia formation. They looked at a wide range of conditions from vomiting and diarrhoea to measles and scarlet fever. They studied a total of 60 individuals with hypoplastic enamel defects and known medical histories, as well as 300 extracted teeth. By dividing the tooth crown in to zones relating to broad periods of development, they were able to relate the various illnesses to the locations of hypoplastic defects in the enamel. However, 51% of individuals studied showed no correlation between known periods of illness and hypoplasia occurrence. Suckling, et al. (1987) also demonstrated the difficulties involved with establishing the specific aetiology of enamel defects. They studied 696 New Zealand children with detailed medical histories available. Fifty six percent of these children had dental defects, but there was limited evidence of any strong associations between known medical conditions and the occurrence of enamel hypoplasia. A similar lack of correlation was found by

El –Najjar, et al. (1978) in their study of modern and skeletal samples from the same region of Ohio.

Congenital syphilis is one of the few diseases that undisputedly produces clearly identifiable dental defects. The disease affects the formation of the crown between birth and one year of age. It produces the characteristic peg like Hutchinson's incisors and mulberry molars in between ten and sixty percent of all patients (Hutchingson, 1858 see Figure 3.4).

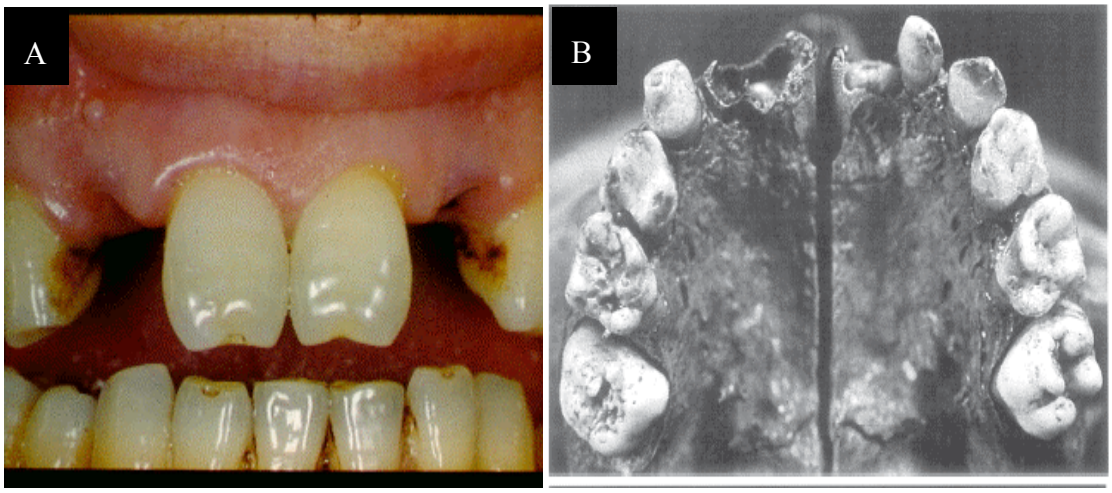

Figure 3.4: Figure showing: A) Hutchinson incisors, and B) mullbery molars.

(From : http://people.eku.edu/savages/385/385.Treponemes.html and

http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0074-02762006001000017&tlng=en&lng=en&nrm=iso).

Toxicity

The most commonly discussed form of toxicity is fluorosis, and there has been a wide range of literature published on the impact of fluoride on enamel growth and

development. There has been much debate about the exact identification and classification of defects caused by fluorosis. Dean (1934) and Zimmerman (1954) both suggest that the defects are graded into six categories, ranging from very mild to severe. This is criticised by Jackson (1961) as the categories are classifying defects on the bases of a presumed aetiology (i.e. fluorosis). Al-Alousi, et al. (1975) developed a recording methodology based on a descriptive index. Today the most commonly used index is that developed by the Federation Dentaire International (FDI, 1982).

In low concentrations, fluoride ions present no damaging effects to enamel formation In fact at low levels (between 0.6 and 1.0 ppm) the inclusion of fluoride into drinking water has been demonstrated to reduce significantly the presence of enamel mottling and subsequently dental caries. Some of the earliest work investigating the impact of fluoride supplementation through water supplies was carried out by Forrest and James (1965). They investigated two populations of children, one from Anglesey where all the children had received fluoridated water, and one from Leeds where the children had not. Thirty nine percent of the Anglesey children had enamel mottling compared to 52% of the children from Leeds. A similar study was carried out by Dini, et al. (2000) which demonstrated that children from a non- fluoridated water region were twice as likely to develop dental carries.

However, if the concentration of fluoride ions in drinking water goes above 1.0 ppm then it can produce detrimental changes in the mineralization of the dental enamel. Fluoride specifically interacts with mineralizing enamel tissue, as it becomes incorporated into the enamel structure, producing florapatite crystals instead of hydroxyapatite crystals (Dobney, 1991). This alters the mineralization process and produces subsurface hypomineralisation. Besten (1999) suggests that this hypomineralised enamel is directly related to a delay in removing amelogenins in the early-maturation stage of enamel formation.

There have also been several studies looking at the impact of excessive fluoride consumption in human and animal populations. Ishii & Suckling (1986) studied 16 Japanese children inadvertently exposed to drinking water containing 7.8 ppm of fluoride. They noted small chalky areas of enamel on the teeth. Wong, et al. (2006) noted a decrease in the frequency of enamel hypoplasia defects from 92% to 35% correlating with a decrease in water fluoridation from 1.0 to 0.5 ppm. Some of the most important studies have investigated excessive fluoride ingestion in animal populations (Kierdorf, et al. 2004; Kierdorf, et al. 2005; Zemek, et al. 2006). These studies looked at the forms that deliberately induced fluoride enamel defects took and at defects occurring naturally in animals living in areas where high levels of fluoride occur due to industrial or environmental pollution.

3.2.3 Trauma

For a long time it was assumed that trauma could cause enamel defects but there was a lack of clinical evidence. Jackson (1961) suggested that the high occurrences of mottling that he noted in incisors could be due to enamel trauma but did not support this suggestion with clinical evidence. Later it was stated by Gerdin (1969a; 1969b) that trauma was an unlikely aetiology for mineralised defects of the enamel. Andreasen, et al. (1971) and Andreasen & Ravn (1973) made a systematic study of trauma and its impact on enamel hypoplasia in Danish school children. In 1973 they identified enamel hypoplasia in the permanent teeth of 57% of children with a history of dental injury to the deciduous dentition, compared to 45% of children with no history of dental trauma. A similar more recent study was carried out by Sennhenn-Kirchner & Jacobs (2006). They studied 106 school children who had suffered damage to their deciduous teeth and noted related enamel hypoplasia occurrence in 25% of these children's permanent teeth.

Suckling and Cutress (1977) investigated the types of enamel defects that were formed when sheep teeth were deliberately traumatised during their developmental period. They directly tested the idea that the stage of tooth development when the

injury occurred had a direct impact on the form the defect took. They operated on successive groups of animals at 4 weekly intervals over the 6 month formation period of the permanent incisors. Of the 18 animals included in the experiment, 14 developed enamel defects. Of these, the only defects which caused the outline of the tooth to be altered occurred during the earliest stages of the tooth bud development. Further experiments ascertained that trauma to the teeth could lead to both missing and hypocalcified enamel (Suckling, 1980) and that this was dependant on the severity of the trauma and whether it produced permanent or temporary dysfunction of the ameloblasts (Suckling & Purdell–Lewis, 1892).

3.3 Hypoplasias and Humans

Enamel hypoplasia has been used in many studies by osteologists as a general measure of population health and status and has been used to investigate a variety of archaeological questions, such as: age at weaning and the development of agriculture.

3.3.1 Frequency of hypoplasia (anthropological and archaeological applications)

Studies on the frequency of enamel hypoplasia throughout the modern world support the general association between living conditions and hypoplasia occurrence, demonstrating a consistent increase of hypoplasia occurrence in individuals living in poor and under-developed regions. Enamel hypoplasias are frequently recorded in children from third world countries. Anderson & Stevenson (1930) indicate that approximately 90% of Chinese children in their study had enamel hypoplasia in some form. Infante (1974) also reported high occurrences (38.9%) of hypoplastic defects in the teeth of children from the White Mountain Arizona Apache reservation, where living conditions were described as being 'near poverty'. This is in stark comparison to children from developed countries where Cutress & Suckling (1982) suggest that frequencies of hypoplasia are likely to fall to below 10%.

Sweeney, et al. (1966; 1969; 1971) more firmly established the link between socio-economic status and hypoplasia occurrence when they studied the deciduous dentition of Guatemalan children. They established that the occurrence of hypoplasia significantly increased with decreasing socio-economic and nutritional status. Infante & Gillespie (1974) also noted a strong correlation between siblings in Guatamalan children, with a 50% increase in hypoplasia prevalence among children with siblings who also had hypoplasia when compared to the rest of the population. This indicates that aetiological factors in this population were operating at a family level. This

strong socio-economic correlation is unsurprising when it is considered that these groups are most at risk from factors such as malnutrition and disease, both factors that clearly influence enamel hypoplasia formation. However, socio – economic status is not always visible in terms of enamel hypoplasia frequency. Oyamada, et al. (2008) investigated class differences in terms of hypoplasia occurrence in Japan in the early modern (Edo) period between the Samurai elite classes and the common classes, but they noted no difference in the incidence of hypoplasia. They suggest that this indicates that the two groups were very similar in terms of nutritional status.

Work by Dobney (1991) compared enamel hypoplasia between socio-economic groups and ethnic groups of school children in Bradford in an attempt to assess the ability to realistically interpret patterns of stress in archaeological populations. His work identified no significant correlations between frequency of enamel hypoplasia and the variables of socio-economic status, adult / infant mortality and unemployment. However, differences in the location and severity of enamel hypoplasia did occur between sexual and ethnic groups. But, surprisingly higher frequencies of enamel hypoplasia were found in White children when compared to Asian children, contradicting local health statistics which indicated that Asian children were of a lower health status than White children. This research clearly demonstrated the multitude of interpretational difficulties faced with investigating archaeological populations. (Dobney & Goodman, 1991)

It is perhaps unsurprising that the frequency of individuals with enamel hypoplasia in archaeological populations is very similar to those found in modern under-developed countries. Goodman, et al. (1984) in their study of the prehistoric Dickenson Mounds populations from Illinois found that 66% of all adults had at least one enamel hypoplasia. Corruccini, et al. (1885) report that 54% of the Caribbean slave populations that they studied had enamel hypoplasia and also suggested that if missing teeth were also accounted for, this number could rise to around 75%. Halcrow & Tayles (2008) also found high frequencies of hypoplasia in prehistoric South East Asia, with 40% of all individuals studied having enamel defects. They

interpret this as evidence for poor maternal and infant health. Temple (2008) studied differences between enamel hypoplasia frequencies in Prehistoric Japan, comparing those from the west where food resources were scarce, to those in the east where they were not. Increased frequencies of hypoplasia were found in the western populations and related to increased systemic / nutritional stress in this population. King, et al. (2002 & 2005) compared enamel hypoplasia in two post medieval populations in London. They identified significant differences between the two populations and suggest that they reflect either: differences in socio-economic status between the two populations or an increase in living standards between the earlier and later populations.

Enamel hypoplasia studies have also been applied to early hominids. Work by Lacruz, et al. (2005) used enamel hypoplasia combined with detailed perikymata counts to suggest that weaning occurred in the Taung Child at approximately two and a half years of age. Enamel hypoplasia have also been used to investigate differences between *Paranthropus*, *Australopithecus* and early *Homo* in terms of enamel development and morphology between these species. Gautelli-Steinberg (2003) identified that *Paranthropus* has significantly fewer enamel hypoplasia per tooth than *Australopithecus* or early *Homo* and suggested that this was due to an abbreviated crown formation span and faster enamel extention rates in *Paranthropus* when compared to *Australopithecus* and early *Homo.* Guatelli-Steinberg, et al. 2004 also investigated differences between Neanderthals and Anatomically Modern foraging groups, as represented by an archaeological sample of Inuit from Alaska. This research indicated very little difference in the stress levels identified through enamel hypoplasia between the two groups (Guatelli-Steinberg, et al. 2004).

One of the main archaeological interests in enamel hypoplasia frequencies has focused on the comparison of hunter-gather and agricultural populations, investigating the transition from one subsistence strategy to the other. Several studies have been carried out investigating this transition, from the Levant (Smith, et al. 1984), Ecuador (Ubelaker, 1984), Peru and Chile (Allison, 1984) and Egypt and

Nubia (Starling & Stock, 2007). All of these studies noted that the occurrence of enamel hypoplasia increases with increasing agricultural intensification, suggesting that intensification of agricultural practises may lead to an increase in physiological stress factors, such as disease and malnutrition. Hypoplasia has also been used to investigate other cultural transitions in human populations. For example, the transition from the Late Antique period to the Early Medieval period was investigated in Croatia using hypoplasia by Slaus (2008). The idea that an increase in enamel hypoplasia frequency can be used to demonstrate increased nutritional deficiencies is also used by Ogilvie, et al. (1989) in their interpretation of high numbers of hypoplastic lesions in Neanderthal teeth compared to modern human populations. However, as discussed above, and pointed out by Neiburger (1990) in response to Ogilvie, et al. (1989), it is important that multiple aetiologies be considered and that malnutrition is not always purported as the sole cause of hypoplastic enamel defects.

Comparing enamel hypoplasia between populations is difficult for several reasons: First, as discussed above, enamel defects can be difficult to classify due to their very varied appearance. This is compounded by the discolouration that commonly occurs over enamel defects. Secondly, hypoplastic defects are highly susceptible to the formation of carious lesions as the enamel is often weaker and the form of the defects often makes cleaning difficult. Thirdly, there is a great deal of variation between the recording standards used in different population studies. These range from a focus on only certain teeth e.g. deciduous incisors, to whether teeth are cleaned or not prior to study. There can also be considerable variation within populations. Ericsson (1955) reported that 20% of Swedish children aged between 14 and 15 years had enamel hypoplasias, whereas only 5% of 7 to 8 year olds showed enamel defects.

There is also an increasing realisation that linking the general health of populations to enamel hypoplasia frequencies is not as straightforward as perhaps was originally assumed (Wood, et al. 1992). For any pathological condition to be visible in the

skeleton the condition has to have been present for long enough for the skeleton to adapt. The presence of enamel hypoplasia in teeth indicates that the individual passed through and survived the insult which caused the hypoplasia. This suggests that the individual was perhaps at a greater advantage than those which did not survive the insult, died, and do not show evidence of enamel hypoplasia. This could be taken further to suggest that a population with high levels of enamel defects may be generally healthier than a population with low levels of enamel defects (King, et al. 2005). However, it is generally considered that enamel hypoplasia is an adequate marker of general population health (Wood, et al. 1992).

While there are difficulties comparing populations recorded using different methods of sampling hypoplastic enamel defects (Goodman & Armelagos, 1985a; 1985b), there does appear to be a consistent relationship between socio-economic status and occurrence of enamel hypoplasia. Although general increases in enamel hypoplasia at the time of weaning in populations indicates that diet is an important contributing factor, there is still uncertainty about its exact contribution and its interactions with other socio-economic factors such as disease. However, wide-scale inter-population comparisons, clearly demonstrate differences in socio-economic status reflected in hypoplasia frequency, even though the underlying reasons (e.g. disease and malnutrition) may be unclear.

3.3.2 Hypoplasia and chronologies

Sarnat and Schour (1941; 1942) were the first to attempt to reconstruct the chronology of systemic stress leading to the production of enamel hypoplasia. Using the process of incremental growth in dental enamel, past physiological stress events or systemic insults could be placed directly within a chronogical framework of an individual's growth and development. Using the crown development chronologies developed by Logan & Kronfeld (1933); Sarnat (1940); Schure & Massler (1940) and Massler, et al. (1941), Sarnat and Schour divided the tooth crown into five periods of growth and development: the prenatal period (4 months *in utero* to birth);

the neonatal period (birth to approximately 2 weeks); the infancy period (3 weeks to 12 months); the early childhood period (13–34 months) and the late childhood period (35– 80 months). In this study Sarnat and Schour established that two thirds of all enamel hypoplasias occurred during the infancy period and that almost all of the remaining third occurred in early childhood.

The chronology developed by Sarnat and Schour (1941; 1942) was generally accepted as applicable to all other human populations (Pindborg, 1970; Yaeger & Sharawy, 1986), even though other detailed skeletal population studies indicated otherwise. Swärdstedt (1966) further developed the methodology of Sarnat and Schour by suggesting that detailed measurement of the locations of each enamel hypoplasia on the tooth crown should be taken, enabling a more accurate chronological assessment of physiological insults (as manifested by enamel hypoplasia) to be established. Swärdstedt's study on a medieval population from Sweden showed that the highest frequency of enamel hypoplasia occurred between 2 and 5 years of age. Schutz & McHenery (1975) also worked on a similar method to Sarnat and Schour (1941; 1942) by dividing the tooth crown into yearly increments. In their study on a prehistoric Californian population, they identified the highest frequency of enamel defects as occurring between 4 and 5 years of age. Hillson (1979) found similar distributions to Swärdstedt (between 2 and 4 years of age) in ancient Nubian and Egyptian material as did Goodman, et al. (1984) in their study of prehistoric populations from Illinois. Corruccini, et al. (1985) also identified peaks of hypoplasia frequency occurring between 3 and 4 years of age in Caribbean slave populations, which they related to the occurrence of post-weaning stress. This association was later supported by Goodman, et al. (1987) who looked at a modern sample of malnourished Mexican children. They identified a peak of enamel hypoplasia occurring between 18 and 36 months, coinciding exactly with the documented age of completed weaning in this population. Finally a re-evaluation of Sarnat & Schour (1941; 1942) by Goodman (1988) on individuals from the Hammond – Todd collection, identified peaks of enamel hypoplasia occurring between 2 and 3 years.

All of this research has indicated that the pattern of enamel hypoplasia formation identified by Sarnat & Schour (1941; 1942) is not universal but varies between populations, both non-industrial and industrial. This may be due to a variety of factors, including differences in growth rates and crown formation between populations, as well as differences in the patterns of exposure to the stressors (such as weaning) which potentially cause enamel defects.

In an effort to create more precise age estimations for enamel hypoplasia formations Goodman and Rose (1990; 1991) suggest the use of a regression formula. This was based on the contention that there was negligible variation in the enamel growth rates between teeth, contrary to the ideas of Massler, et al. (1941) which had formed the basis for earlier chronological studies. However, Goodman and Rose (1990; 1991) do not include cuspal enamel formation times in their equations and this may lead to significant underestimation of the age at which enamel hypoplasia is formed (Skinner & Goodman, 1992; King, et al., 2002). Goodman and Song (1990) however, argue that not including cuspal enamel formation rates increased age estimations by no more that six months. Using regression equations also heavily relies on the assumption that enamel growth is linear, and it has been repeatedly demonstrated that this is not the case (Skinner & Goodman, 1992; Goodman & Song, 1990; King, et al., 2002).

More recently, researchers have begun to use microscopic / histological approaches to estimate the age at which enamel hypoplasia occurs (Hillson, 1992a; 1992b; 1992c; Hillson & Bond, 1997; King, et al, 2002; 2005). These methods focus on quantifying the spaces between individual perikyma and calculating the days that these would have taken to form. This deals with the problem of assuming linear enamel growth as well as differences between populations in terms of tooth crown size. However, this method is time consuming and destructive (Ritzman, et al. 2008). Reid and Dean (2000, 2006) take microscopic age estimation one step further. Using microscopic methods, they divide the crown height into equal tenths and then

calculate the time taken for each tenth to develop. Ritzman, et al. (2008) and Martin, et al. (2008) both compare the results gained from using this method to those gained from the earlier regression methods of age estimation. Ritzman, et al. (2008) conclude that the two methods produce substantially different results, large enough to lead to different interpretations of the bio-cultural factors causing the enamel hypoplasia formation. They go on to suggest that earlier studies looking at enamel hypoplasia chronologies should be re-evaluated using microscopic methods similar to that used by Reid and Dean (2000, 2006). Martin, et al. (2008) suggest that the differences produced are statistically significant but that they should not affect the bio-cultural interpretation of the results as it is 'broad time' and not 'precise time' occurrence patterns that are important in archaeological interpretations.

3.3.3 Markers of stress

There has been some research looking at the relationship of enamel hypoplasia with other indicators of general stress. Obertova & Thurzo (2008) investigated the relationship between enamel hypoplasia and cribra orbitalia (a physiological indication linked with anemia). They noted the occurrence of both conditions in 11% of individuals studied, and conclude that several factors such as diet influences the occurrence of the two conditions. It is general practice in physical anthropology to record both the prevalence and the severity of enamel hypoplasia (Buikstra & Ubelaker, 1994; Hillson, 1996). Both these factors are widely used to make assessments of general stress levels in both human and animal populations (Goodman & Rose, 1990; Hillson, 1996; Lukacs, 1999; 2001; Franz-Odendaal 2004).

Goodman and Rose (1990) and Dobney and Goodman (1991) propose that there is a 'threshold', which once passed prevents the ameloblasts from functioning at a normal level, leading to hypoplasia formation. Figure 3.5 shows the combinations of possible factors which could cause enamel hypoplasia to form, including unknown etiological and susceptibility factors, nutritional intake and illness history. Clearly

there are combinations of underlying factors (nutrition, susceptibility and illness) which govern the formation of enamel hypoplasia. The result of this is that individuals or populations that have increased levels of these factors will be closer to the threshold of hypoplasia formation and subsequently a milder stress impact will produce an enamel defect, whereas in an individual / population with lower levels of these factors the same stress would not produce an enamel defect.

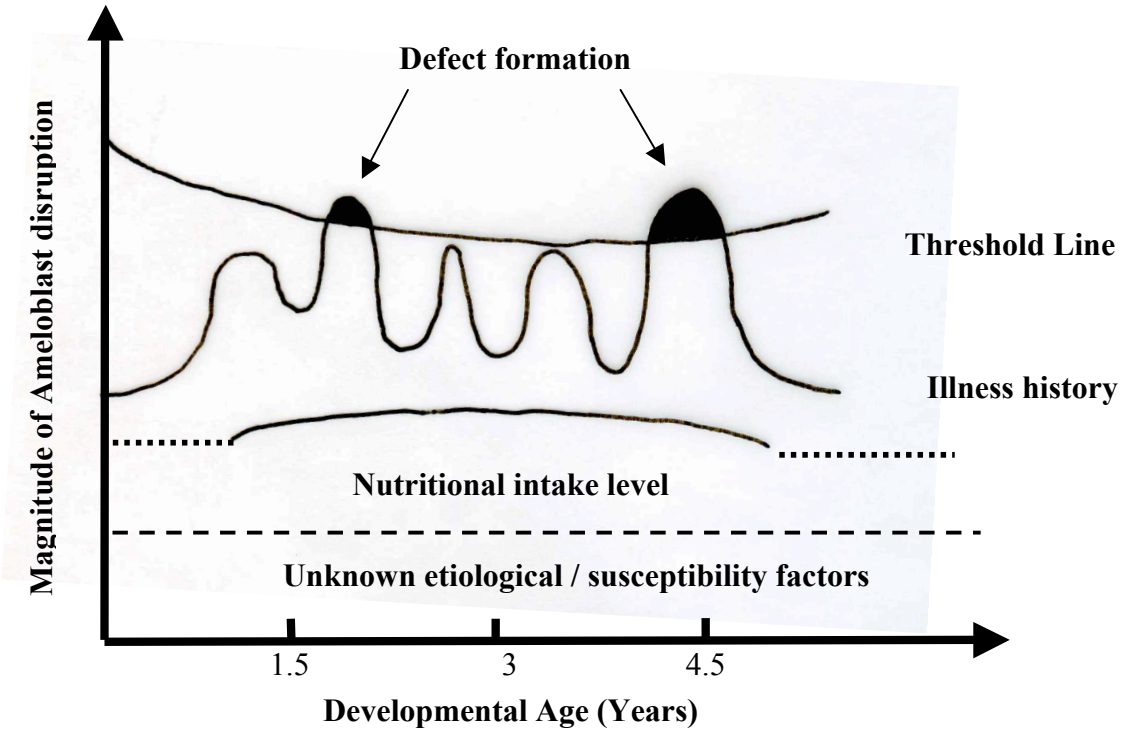

Figure 3.5 : Stress threshold model (from Goodman & Rose 1990 : 75). Stress threshold line is curved, reflecting the high susceptibility of ameloblasts to stress in the middle phase of their secretory cycle.

Kierdorf, et al. (2004) and Witzel, et al. (2006 & 2008) propose that there are in fact three different thresholds that can be crossed, each producing slightly different enamel defects. The lowest of these thresholds produces just a slight reduction in the

secretion of enamel matrix but does not affect the Tomes process. This leads to enamel with a normal microstructure but a reduction in the spacing between the striae of Retzius, leading to the formation of depression-type defects. When the second threshold is passed the ameloblasts are affected to the extent where they can no longer maintain the distal portion of the Tomes process, leading to the production of aprismatic enamel. When the uppermost threshold is passed the ameloblasts completely cease matrix production, leading to pit, line and plane-type defects (Witzel, et al. 2008). They go on to suggest that there are two factors which affect the severity of enamel defects. The first is the intensity and duration of the insult and the second is the differential response of the ameloblasts depending on their secretory stage. The two studies by Witzel, et al. (2006; 2008) demonstrate that the different types of hypoplasia formed (i.e. line, plane and depression) can be related to the different severities of stress causing them. Depression-type defects are related to low level, long period stresses; lines and pits to short term moderate level stresses, and plane-type defects to short – long term severe insults.

3.4 Enamel Hypoplasia and animals

As is obvious from the preceding text, the bulk of research carried out on enamel hypoplasia has been focused on modern and ancient human populations. There have, however, been a small number of studies carried out using animals.

3.4.1 Non-domestic animals

In modern animal studies, hypoplasia has proved to be a useful indicator of development stressors. Franz-Odendaal (2004) investigated differences between wild and captive giraffes (*Giraffa camelopardalis*) using the occurrence of enamel hypoplasia. Her results showed that wild giraffes exhibited no signs of enamel hypoplasia, suggesting that wild giraffes suffer considerably lower levels of systemic stress than their captive counterparts. The captive giraffes showed periods of physiological stress (indicated by the occurrence of hypoplastic defects of enamel) at six months, three years and again between four and five years. The first of these events was linked to weaning but suggestions were not made for the possible causes of the later defects.

The use of enamel hypoplasia in human populations as an indicator of general stress has recently prompted a wide range of studies to investigate enamel hypoplasia in non–human primates, and there has been much research into the great apes, specifically exploring the differences in prevalence of enamel hypoplasia between species (Guatelli-Steinberg, 2000; 2001; Guatelli-Steinberg & Lukacs, 1998; Guatelli-Steinberg & Skinner 1998; 2000; Moggi-Cecchi & Crovella, 1991; Newell, 2003). Lukacs (1999; 2001) investigated the prevalence of enamel hypoplasia in chimpanzees, gorillas and orangutans. He discovered that the large bodied apes (gorillas and orangutans) showed a higher frequency of enamel hypoplasia than chimpanzees and suggested that this may be due to greater physiological stress in the peri and post natal development period of the larger bodied apes.

Skinner and Hopwood (2004) carried out a detailed study into the causes and periodicity of enamel hypoplasia also in chimpanzees, gorillas and orangutans. They concluded that physiological stress (demonstrated by the presence of enamel hypoplasia) began at approximately two and a half years of age and continued in a regular episodic manner. They were able to relate these stress episodes to fluctuating seasonal / environmental factors, leading to increasing mild malnutrition and disease. They also noted that, as in the previous study, gorillas and orangutans had higher levels of enamel hypoplasia than chimpanzees.

From these studies it has become clear that the frequency of enamel hypoplasia increases in direct relation to the size of primate, with frequencies being lowest in the prosimians, rising through the new world monkeys, old world monkeys and finally the great apes (Guatelli-Steinberg, 2000; 2001; Miles & Grigson, 1990; Moggi-Cecchi & Crovella, 1991). More recent studies investigating the differences between the occurrence of enamel hypoplasia in the great apes have begun to suggest that differences in crown height (and subsequently development periods) may be partly, if not fully, responsible for the observed differences between the large bodied and smaller bodied apes (Guatelli-Steinberg & Skinner, 1998). With the longer developmental periods in larger bodied apes producing an extended time frame in which stress events can be recorded in the dentition (Guatelli-Steinberg, 2000; 2001). Newell, et al. (2006) go on to suggest that the theory of a 'wider developmental window' should also be combined with detailed analysis of the internal structure of the tooth. They demonstrate that in large crowned species the striae of Retzius shift as they are compressed into the more slowly growing cervical half of the crown. As they are compressed, the spaces between them become narrower and their angle with the dentine enamel junction becomes wider. This leads to the formation of deeper imbricational lines (perikyama), which make pathological striae (mild line-type enamel hypoplasia) more obvious than when they are in the occlusal half of the crown (Newell, et al. 2006).

Other studies have explored the impact of nutrition and environmental change on enamel hypoplasia occurrence and frequency. Collet and Teaford (2008) explored very similar hypotheses to that carried out in the research detailed in this thesis – i.e. relating external environmental conditions to enamel hypoplasia occurrence in *Cerbus* monkeys. They examined the idea that higher frequencies of enamel hypoplasia can be related to increases in environmental stress. They studied 38 *Cebus* monkeys from 15 locations across Brazil and correlated the frequency of enamel hypoplasia to the amount of rainfall occurring in each region. As water availability is associated with high levels of bio-availability and subsequently to nutritional resources, areas with high levels of rainfall were considered to be less environmentally stressful and it was hypothesized that monkeys from these areas would show lower levels of enamel hypoplasia occurrence. This hypothesis was supported by their results, which demonstrated that *Cerbus* monkeys from savannah and scrub land exhibited significantly higher levels of enamel hypoplasia than animals from rainforest or costal regions. Nutritional stress was also investigated in Rhesus monkeys (*Macaca mulatta*) by Guatelli-Steinberg and Benderlioglu (2006), who investigated a population of isolated monkeys on the island of Caya Santiago. These animals were reportedly in poor health until a feeding program was instituted in 1956. Enamel hypoplasia frequencies were calculated for animals from both before and after the feeding program was introduced, the authors noted a statistically significant decrease in enamel hypoplasia occurrence after 1956.

There has also been a series of studies investigating enamel hypoplasia in Pleistocene and early Holocene bison (Niven, 2000; Niven, et al. 2004; Byerly, 2007). These papers suggest that enamel hypoplasia in Pleistocene and early Holocene bison can be potentially related to a range of regular seasonal stresses including post-rut nutritional deficiencies, weaning, cold-season forage quality and availability and seasonally dependent mineral deficits.

3.4.2 Domestic animals

The only investigations into domestic animals have been carried out on archaeological and modern wild and domestic *Sus* (Dobney & Ervynck, 1998, 2000; Dobney, et al. 2002; 2004; Ervynck & Dobney, 1999; Ervynck, et al. 2001; Dobney, et al. 2007; Rowley-Conwy & Dobney, 2007; Dobney, et al. 2005). These studies clearly demonstrate that in both wild and domestic *Sus* populations, enamel hypoplasia can be related to key physiological events such as birth and weaning, as well as to seasonal events that can impact upon nutritional and health status.

By comparing populations of pigs from Neolithic and medieval sites across a wide range of regions, Ervynck and Dobney (1999) demonstrated that changes in environmental conditions (such as deforestation) and animal husbandry practices (such as intensive rearing) could adequately explain differences in general prevalence rates of enamel hypoplasia between sites. They also demonstrated the potential for enamel hypoplasia to indicate changes in livestock management, such as age at weaning, stalling, double farrowing, seasonal changes in the availability of food and domestication.

In a later study (Ervynck, et al. 2001), frequencies of enamel hypoplasia were used to assess the domesticated status of pigs from the Neolithic site of Çayönü Tepesi, south-eastern Anatolia, Turkey. It had long been assumed that this site represented one of the earliest domestication centres for the pig in western Asia. The analysis of hypoplastic dental lesions (in tandem with biometrical evidence – principally measurements of tooth crowns) showed a gradual increase in frequency over time, suggesting a very gradual transition from wild to domestic status. The results of this study were further supported by Dobney, et al. (2004) in their investigation into recent and archaeological populations in north-west Europe focusing of the effects of early domestication. They identified consistently high frequencies of enamel hypoplasia in both modern and archaeological domestic pig samples, compared with low frequencies in modern and archaeological wild boar populations from the same regions. They suggest the high frequency of enamel hypoplasia identified in recent

and archaeological domestic populations are the result of animal husbandry pressures. They also suggest that variation seen between populations is the result of differences in animal husbandry regimes, ecological conditions and the various proportions of wild boar present in the data-sets. They concluded that 'in general higher frequencies of (enamel hypoplasia) in ancient pig populations can be broadly explained by direct or indirect human interference in the form of domestication and husbandry' (Dobney, et al. 2004: 206).

This work is further supported by Dobney, et al. (2007) and Rowley- Conwy & Dobney, (2007) in studies of the transition from wild to domesticated pigs in Eurasia. These two papers demonstrated that enamel defects were more prevalent in all archaeological populations studied than their recent wild counterparts. Despite increasing human interference wild populations continued to show low frequencies of enamel hypoplasia. Dobney, et al, (2007) suggest that this trend, again used in tandem with biometric evidence of variation in tooth size over time indicates 'a long drawn-out domestication process' (Dobney, et al. 2007: 82).

3.4.3 Enamel hypoplasia in caprines

There has been extensive experimental work carried out by Suckling, et al. looking at the variety of causes of enamel hypoplasia in recent caprine populations. (Suckling & Cutress, 1977; Suckling, 1980; Suckling & Purdell-Lewis, 1982; Suckling, et al. 1983; Suckling, et al. 1984; Suckling, 1986; Suckling et al., 1986). In these studies enamel defects were artificially induced in sheep by either causing trauma to the developing tooth bud or by infecting the animals with high doses of parasites. Unfortunately all of these defects were induced in the incisor teeth of sheep, providing little or no information about the formation of enamel defects in the permanent molars. However, these papers provide an important baseline of information about the levels of parasitic infection and other such conditions needed for enamel defects to form.

There are two other published studies of enamel hypoplasia in caprines. The first by Arbuckle (in press) studies the caprine remains from two Neolithic villages in central Anatolia (Çatalhöyük and Erbaba). The methods used were developed separately to those developed in this research, but were based on the same methods produced by Dobney and Ervynck (1998). The differences between the two methods are fully outlined in Chapter 4. The study by Arbuckle (in press) identified enamel defects in both populations and tentatively related them to the occurrence of seasonal nutritional stress.

The second paper is by Balasse, et al. (in press see Appendix 1) and is discussed in more detail both in the following chapter (in terms of methodological approaches) and in Chapter 6. In this paper we studied a modern sample of caprines from Kenya. The paper demonstrated that there was a significant difference in the frequency of enamel hypoplasias between sheep and goats from the same region. We suggested that this was due to differences in consumption methods between the two species, with the ability to browse from a range of food sources making goats less-susceptible to the rarefaction of grassy resources in drought periods. In this paper we also demonstrated that caprines from the drier region studied displayed both a higher frequency and an increased severity of enamel hypoplasia than caprines from the more mesic region. We suggest that this difference is a reflection of more fragile balance of the herding systems within this environment.

All of the work discussed in this chapter has provided vital background information on the potential causes, internal formation, recording and analysis of enamel hypoplasia in various species and populations. This thesis builds upon much of the work outlined in this chapter, particularly on the recording and interpretative methods of Dobney & Ervynck (Dobney & Ervynck, 1998, 2000; Dobney, et al. 2002; 2004; Ervynck & Dobney, 1999; Ervynck, et al. 2001). The work discussed above by Arbuckle (in press) and Balasse, et al. (in press) also provided useful key insights, approaches and data into the viability of enamel hypoplasia studies in high crowned species – specifically caprines. Both papers demonstrate that enamel

hypoplasia occur in caprine populations and are recordable. The paper by Balasse, et al. (in press) also clearly demonstrates that enamel hypoplasia in caprines can be linked to environmental and nutritional stressors.

Whilst enamel defects can be used as a general stress marker, the work carried out by Suckling (Suckling & Cutress, 1977; Suckling, 1980; Suckling & Purdell-Lewis, 1982; Suckling, et al. 1983; Suckling, et al. 1984; Suckling, 1986; Suckling, et al. 1986) investigated possible aetiological factors in sheep such as parasitic loading and trauma. Other early experimental work on animals investigated a huge range of factors which can cause enamel hypoplasia, providing essential information on the range of conditions leading to enamel defect formation. The early work carried out on human populations, researching the frequency and chronology of enamel defects has also been essential in providing a background understanding of the potential uses of enamel hypoplasia in population based studies. Finally, work by Kierdorf, et al. (2004) and Witzel, et al. (2006, 2008) has allowed a more detailed understanding of the complex internal dental structures that affect the formation of enamel hypoplasia. All of these studies in enamel hypoplasia have provided essential information about the application of enamel hypoplasia studies in a variety of species for understanding past populations. Each has explored a range of approaches and techniques to the recording and interpretation of enamel defects in a range of human and animal species, all of which underpins the following study.

4 Developing a methodology and dental chronology

In this chapter, previous methodological approaches developed for recording enamel hypoplasia in various species are discussed, along with some of the problems and challenges of recording enamel hypoplasia in high crowned species. The methodological approaches employed in this research are then presented using supporting data from caprine populations analysed in this thesis. Using enamel histology and modern caprine assemblages this chapter then explores the growth, development and chronology of caprine teeth, an aspect essential to the successful interpretation of enamel hypoplasia. Finally methods for analysing and interpreting enamel hypoplasia data recorded in this study are explored in more detail. Some of the methodological approaches discussed in this chapter were produced in close collaboration with Dr Marie Balasse and Dr Anne Tresset (Centre National de la Recherche Scientifique, Paris), whilst the histological analysis was carried out in close collaboration with Professor H. Kierdorf, Dr U, Kierdorf and Dr C. Witzel (University of Hildesheim, Germany).

4.1 Previous methodologies for recording hypoplasia

There have over the years been multiple attempts at distinguishing and classifying hypoplastic lesions in dental enamel, mainly focusing on humans (e.g. Berten, 1895; Stones, 1966; Schultze, 1970; Pindbourg, 1982; Sarnat & Moss, 1985; FDI, 1982). As discussed in the previous chapter, many of these classifications have focused on aetiological factors, making them difficult to easily apply. Of the methods created for recording hypoplastic defects, there are two that are most useful. The first classification is based upon descriptions by Berten (1895), where enamel hypoplasias were divided into three types: ‘little pits’, ‘furrows’ and ‘plane forms’ and these

categories have remained as the basic classification of hypoplastic defect types to this day. The second was developed by the Federation Dentaire International (FDI) who in 1982 proposed a system of classifying all dental defects. Opacities were divided by colour into cream/white and yellow/brown and classed as defect types 1 & 2 respectively. Hypoplastic defects were classified as pits (type 3), horizontal grooves (type 4), vertical grooves (type 5) and total absence of enamel (type 6). The number and demarcation of defects were classed as single or multiple and diffuse, fine lines, diffuse or patchy (FDI, 1982). In order to record the location of the defect the tooth was divided into sections: Gingival half, incisal half, occlusal and cuspal. This system has been one of the most widely used classification and recording systems, particularly with regard to the recording of enamel hypoplasia in modern human populations. Because the FDI system provided one of the first clear and concise methodologies for the recording of enamel hypoplasia, it provides the basis for almost all other systems ever developed. However there are some problems associated with this system, such as the lack of detailed descriptions to accompany the defects types. This makes identifying some of the defects described, particularly 'vertical lines', challenging.

In terms of methodologies for recording enamel hypoplasias on animal teeth, the system devised by Dobney and Ervynck (1998) recording enamel hypoplasia in pigs has provided the basic model for much of the current research into enamel hypoplasia in animals. Three main types of hypoplasia (lines or grooves, depressions and pits) were identified and a simple recording system was set up whereby the location of the enamel defect was measured vertically from the fixed point of the root enamel junction (REJ) to the lowest point of the enamel.

Three key papers have investigated aspects of recording enamel hypoplasia in high crowned species, Niven, et al. (2004); Balasse, et al. (in press) and Arbuckle (in press). Niven, et al. (2004) investigated enamel hypoplasia in Late Plains Archaic bison populations. Defects were recorded on the both buccal and lingual tooth surfaces and measured from the lowest point of the root enamel junction to the centre of each defect. Modern bison teeth and radiographs were then used to estimate the rates of enamel growth and dental chronology. The monthly enamel growth rates

were then used to plot enamel hypoplasia into calendars of dental development. The methodology used by Niven, et al. (2004) fails to take into account the possibility of variation in enamel growth rates down the tooth crown and dental wear removing the enamel hypoplasia in the occlusal portion of the tooth.

In the paper by Balasse, et al. (in press) we present the findings of a study into enamel hypoplasia in modern caprines from Kenya. The recording methodology used is a preliminary version of the one outlined below, based on the methodology developed by Dobney and Ervynck (1998) but altered to adjust for caprine populations. The only difference in the recording methodology used in the paper and that presented here, is the inclusion of maxillary molars in the study, something which is not done in this thesis (for the reasons outlined below). However, some key differences exist in the methodology regarding data analysis and interpretation. In the paper we do not consider the possibility of variation in enamel development rates down the tooth crown or use running means analysis to smooth the data.

Arbuckle (in press) presents a methodology for recording enamel hypoplasia in caprines, also based on the methodology developed by Dobney and Ervynck (1998) and the FDI (1982). This methodology was developed separately but at the same time as the methodology outlined in this study and used by Balasse et al. (in press). Consequently there are some clear differences in the approaches. Arbuckle's study focused on only isolated mandibular molars, a function of the fragmented nature of the archaeological assemblages being studied. Defects were recorded on both the buccal and lingual surfaces based on the Federation Dentaire International system discussed above. Defects were also recorded on a three point severity scale, ranging from light, moderate to severe. The location of the defect was measured from the point of the defect closest to the occlusal surface down to the REJ, which is standard practise in the recording of enamel defects (Niven, et al. 2004). Arbuckle attempts to overcome the problem of dental wear preventing an accurate assessment of complete crown height (discussed in detail below) by adding an arbitrary 33% onto the average crown height for each molar, this is further extended in the first molar (commonly exhibiting the most severe wear) by adding 'several millimetres' to the maximum height recorded for first molar (Arbuckle, in press: 17).

There are several identifiable problems with the method created by Arbuckle (in press). The focus on isolated teeth, whilst resolving the issues surrounding tooth visibility when still in the mandible (discussed below), raises complex interpretative issues regarding the separation of isolated first and second molars in archaeological caprines. Given that defects should theoretically appear equally on both buccal and lingual surfaces, there is no real need to record both surfaces, and doing so increases the risk of data duplication. Arbuckle also fails to address the potential problems of coronal cementum, which can seriously obscure the enamel surface and therefore, enamel defects from view. However, perhaps the main limitation with Arbuckle's methodology is in the methods used to combat the problems associated with dental wear. It is felt that adding an arbitrary 33% to the maximum tooth height for each molar recorded is not an accurate enough method of dealing with this complex issue. This is especially true for the first molar, which Arbuckle rightly notes is subject to more extreme wear. However the addition of an un-quantified number of millimetres to the crown height cannot be regarded as a viable way of systematically dealing with this problem within and between datasets, and severely limits the important use of comparative approaches to data analysis and interpretation.

4.2 Problems with the visibility of enamel hypoplasia in Caprines

Animals with brachydont (low crown) dentition, especially humans, have been the main focus of previous methodological approaches to the study of enamel hypoplasia as discussed in Chapter 3. This is because high crowned (hypsodont) teeth pose a series of problems to the study of enamel defects, chief amongst which are rates of dental wear, tooth length, and the presence of coronal cementum. All of these issues potentially affect the accurate recording of enamel defects, consequently it is vital that this research addresses and overcomes these issues.

4.2.1 Coronal cementum

As discussed in Chapter 2, the key role of cementum is to hold the tooth within the jaw, providing a firm attachment for the periodontal ligaments, which are attached to the alveolar bone surrounding the tooth. This anchors and supports the tooth as the various pressures of mastication are exerted on it. In low-crowned species the tooth erupts fully-formed into the mouth cavity. Once the enamel is fully-formed, it is protected until it erupts, by a layer of ameloblasts, which, once they have secreted and mineralised the enamel, cover and protect its surface from the surrounding cementocyte cells. Consequently, in low-crowned species cementum forms only on the tooth root and not over the enamel, however, in high-crowned species the teeth begin to erupt into the mouth and come into wear before the tooth roots are formed, leaving a large portion of the tooth crown still buried in the alveolar bone. Once eruption begins, the ameloblasts protective barrier is broken, leaving the buried enamel surface exposed to the surrounding cementocyte cells. These cells then begin to secrete cementum over the enamel surface. The lack of root development in these early stages of eruption in high-crowned species means that the cementum plays a vital role in anchoring the tooth into the bone and acting as support until the tooth root is developed. Cementum also plays a vital role in holding the tooth in the jaw as progressive eruption of the teeth compensates for the constant shortening of the tooth crown due to dental wear (Kierdorf, et al. 2006).

Cementum on high crowned teeth can consequently cause a variety of problems for recording enamel hypoplasia; the first being that cementum is deposited in layers. Variation in these layers and their thickness can result in the formation of a ridged surface, which can mimic enamel hypoplasia defects. While these ridges in the cementum can be related to underlying 'true' enamel defects, it can also be the case that the enamel below the cementum is free of defects and the ridges are only present in the cementum (see Figure 4.1). This can potentially cause serious problems in the accurate recording of enamel hypoplasia in high crowned species, as pointed out by Kierdorf, et al. (2006) in their criticism of work by Niven, et al. (2004) who record imbricational lines in cementum as enamel defects in their study of Pleistocene and early Holocene bison. It is thought that the formation of these imbricational cementum layers relate to periodic tooth uplift caused by dental wear and eruption, which lead to the periodic deposition of new layers of cementum (Kierdorf, et al. 2006). The second, and perhaps most obvious, difficulty caused by the presence of coronal cementum, is that it covers the enamel surface, potentially obscuring hypoplastic enamel defects entirely (as clearly demonstrated in Figure 4.2) - or at least masking their true depth and size and therefore making accurate scoring of presence, position and severity extremely difficult.

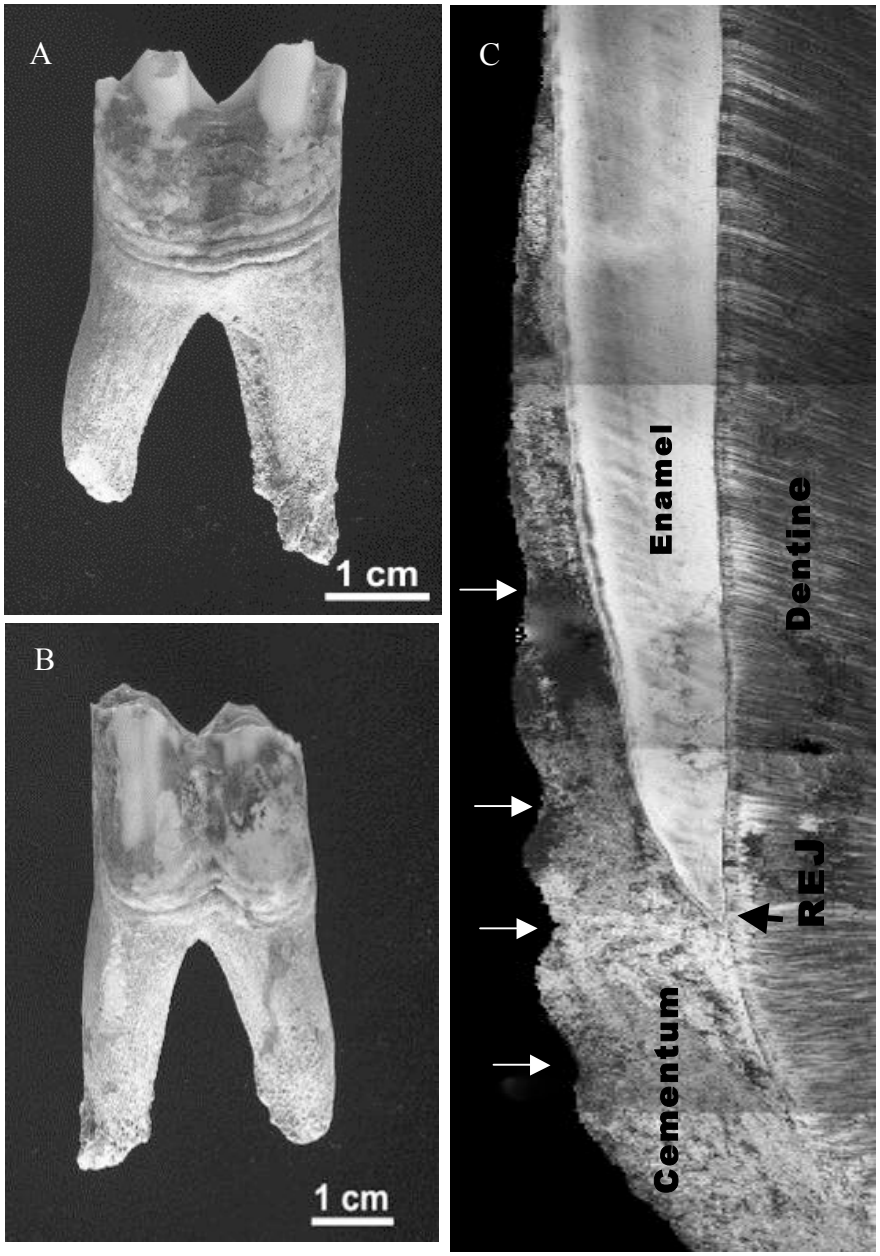

Figure 4.1: A cattle 1st molar with clear lines in the cementum. A = lingual view; B = buccal view; C = axiobuccolingual ground section though this tooth viewed in normal transmitted light, clearly showing lines (indicated by white arrows) are occurring only in the cementum (after Kierdorf, et al. 2006).

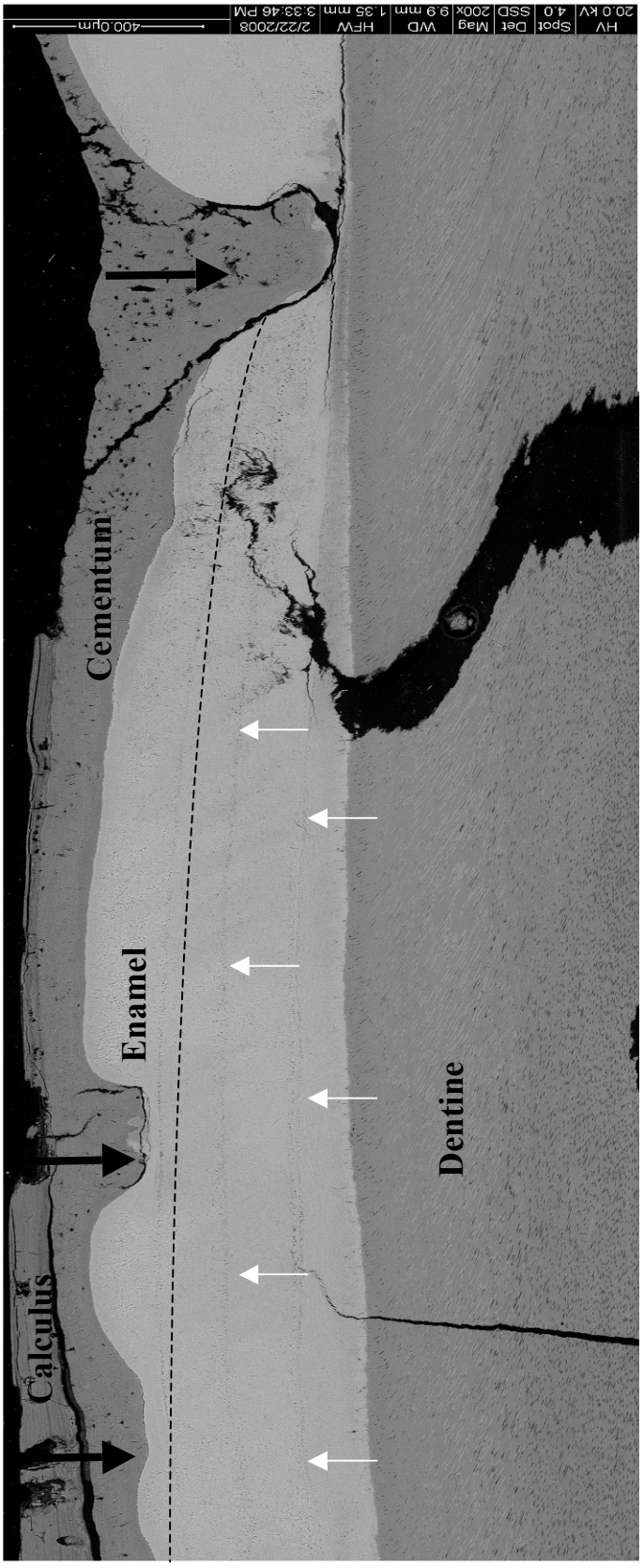

Figure 4.2: An axiobuccolingual ground section SEM through part of a caprine second molar from Kenya (Oloi o/c 2) showing how a combination of coronal cementum and calculus have completely obscured a series of dental defects. The occlusal surface is located to the left and the REJ is located to the right of the image but neither is shown. Black arrows mark the location of the enamel hypoplasia, completely obscured by a combination of cementum and calculus. The dotted line indicates the line followed by one of the pathological striae of Retzius underlying the enamel hypoplasia, the line of two other pathological striae are identified by white arrows. (modified section image from Witzel, Unpublished).

Fortunately the covering of coronal cementum in caprine teeth is considerably thinner than that of larger high-crowned taxa such as bovids or equids, meaning that hypoplastic defects are more commonly visible through the cementum (Figure 4.3). This also means that there is less opportunity in caprine teeth for clear imbricational layers to develop in the cementum (as shown in a cattle tooth in Figure 4.1 above). For this study, caprine teeth in which the coronal cementum appeared particularly thick, or in which it could not be established if the defects occurred in the underling enamel, were excluded from the analysis. Histological analysis carried out on teeth from two of the modern caprine populations studied (North Ronaldsay and Kenya), demonstrated that coronal cementum covers the tooth crown in all of the samples studied (even when the enamel surface appears to the free from cementum as shown in Figure 4.3). Therefore coronal cementum will almost certainly affect the recording of enamel hypoplasia equally in all caprine populations.

While this research has not fully 'solved' the problem of coronal cementum, it demonstrates that the effects of coronal cementum in caprines are likely to be minimal, affecting all caprine populations equally. As a result, potential comparative bias within and between datasets will be minimal. It is certain that some enamel defects will be invisible on the tooth surface due to a thick cementum covering and therefore not recorded. It is also certain that some severe defects will be given a lower severity score as their true depth will not be visible due to cementum layers. However, all populations will be equally affected by this, producing a consistent number of 'invisible defects' and consistent under-scoring of defect severity.

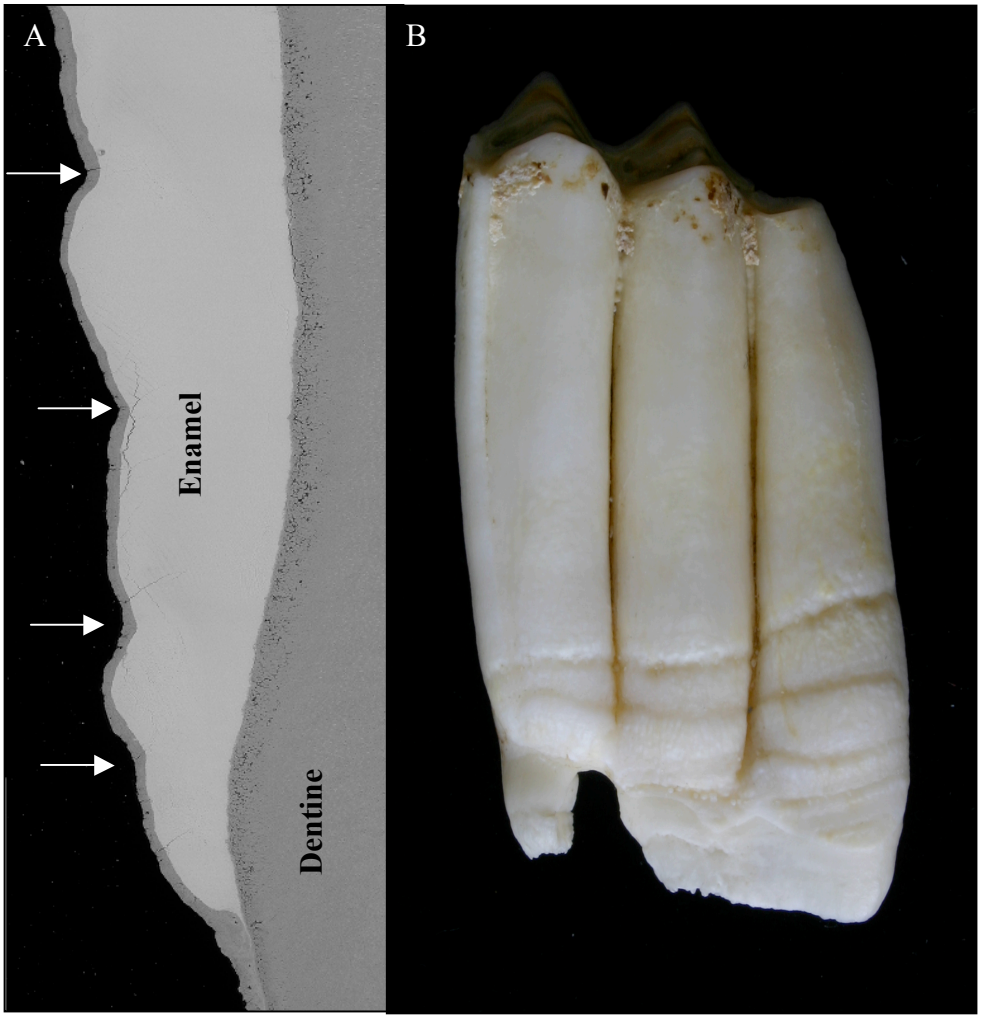

Figure 4.3: A thin section (A) through the posterior cusp of a right third molar (B) from a North Ronaldsay sheep (NR 84.126). Although the enamel surface is completely covered in coronal cementum, visible as a thin grey line over the surface of the enamel in image A, the defects (indicated with white arrows) are still clearly visible and recordable (thin section image and photograph of molar by Witzel, unpublished).

4.2.2 Dental wear and tooth length

As discussed above, the teeth in high-crowned species undergo extreme dental wear. This can cause difficulties in recording enamel hypoplasia, as the constant tooth wear can potentially remove a large part of the occlusal portion of the crown, destroying any hypoplasia occurring in this area. This means that if large numbers of worn teeth are studied, the data may be biased towards enamel defects occurring only in the cervical half of the tooth crown.

The second problem posed by high-crowned species, as indicated by their name, is the length of the teeth themselves. In low-crowned species the entire crown of the tooth erupts into the mouth leaving only the root hidden within the mandibular corpus. However the long developmental rates and constant wear and eruption of high-crowned species teeth means that a large percentage of the enamel crown is not visible, making any hypoplastic defects impossible to see, except those present on the upper most (erupted) portions of the tooth (See Figure 4.4).

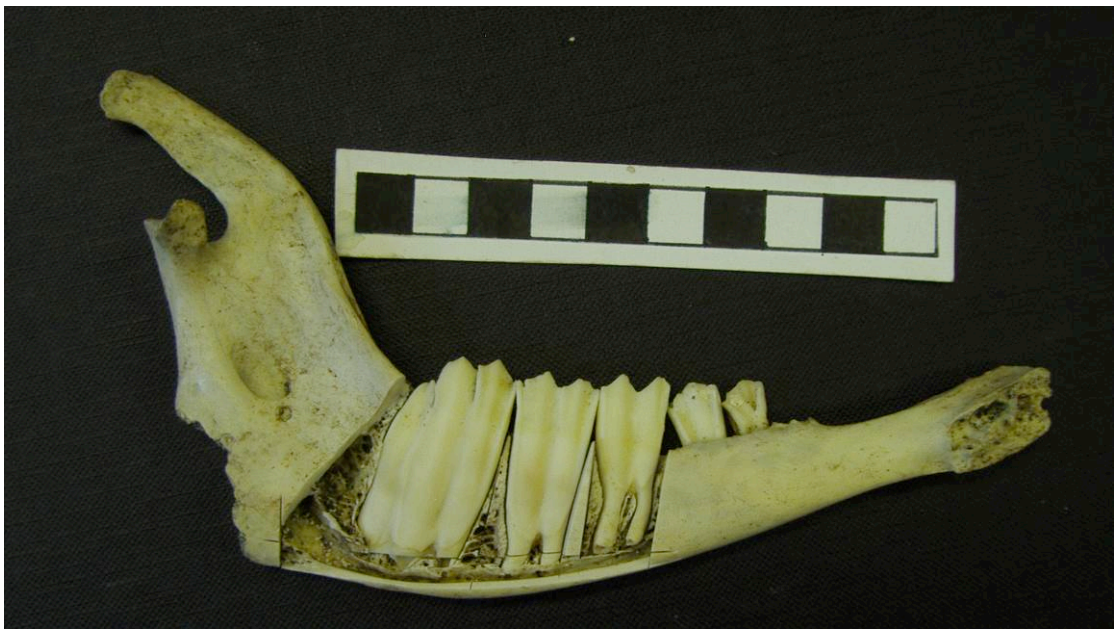

Figure 4.4: Showing the large amount of tooth crown hidden inside the mandibular corpus of caprines.

As discussed above, dental wear potentially poses a series of problems to the analysis and interpretation of enamel hypoplasia in caprines. As outlined in more detail below, mandibles from Payne age classes C (6-12 months) to F (3-4 years) are preferentially used in this study. These age classes cover the complete dental development of all three molars and provide a range of wear stages from the very early wear through to more advanced stages, where several millimetres of the upper portion of the crown have been removed.

Dental wear was investigated in several of the modern populations, discussed in later chapters (mainly populations from North Ronaldsay and Hoy discussed in Chapter 5). These preliminary studies into dental wear and enamel hypoplasia, revealed several important facts: Studies on the modern material from North Ronaldsay and Kenya clearly demonstrated that the upper half of the molar crowns rarely contained enamel hypoplasia, regardless of tooth wear (see Figure 4.5 and Figure 4.6). This data clearly demonstrated that while dental wear does remove the upper potions of the tooth crown, the amount of tooth lost is a very small percentage of the total height of the tooth crown, and rarely contained hypoplastic defects. This research indicated that as long as there was adequate representation of teeth in early wear stages (e.g. Payne age stage C) to check for enamel hypoplasia in the upper portions of the tooth crown, there was little chance that recording teeth in more advanced wear stages would significantly bias the location of enamel hypoplasia to the lower half of the crown.

In the smaller archaeological data sets, this meant that as long as young animals were present in the assemblage, representing the early wear stages, older animals (G +) could also be included in the analysis. Not restricting the data-sets to individuals from just the younger age classes was useful for several reasons. Firstly, the majority of archaeological material studied did not present as complete tooth rows - making the identification of definitive age classes difficult. Secondly, the archaeological assemblage often consisted of small amounts of material for study and it was important to gain as much data as possible from this. For these reasons, in small archaeological assemblages where a range of mandibles at different developmental ages were available for study, only exceptionally worn tooth crowns (where there

was less than 10mm of crown remaining) need be (and were) excluded from further analyses.

Where possible, this research has focused upon complete molar rows, dealing with the issues surrounding the use of isolated teeth and the accurate separation of first and second molars. In order for the hypoplasia to be recorded in complete mandibular tooth rows, the teeth were extracted from the mandibular corpus and cleaned to allow total visibility of the enamel surface. Teeth were extracted from the mandible using a diamond-edged dental drill identical to those used by dentists. Ideally the jaw bone was removed in three or four neat sections (one over each tooth with a long cut running along the mylohyoid channel: see Figure 4.7) but practically this was not always possible due to a variety of factors which included differing root depths, alveolus thickness between the teeth and preservation of the mandibles. Bone which had been badly weathered tended to be much more friable and prone to breaking into multiple fragments, whereas more modern bone with higher collagen content was much easier to extract.

The bone was always removed from the mandible on the lingual side, where the jaw is thinner. Unlike the situation in pigs reported by Dobney & Ervynck (1998), the lingual side of the tooth also showed less evidence of hypoplastic defects and so was not included in the recording protocol (this is discussed further below). This meant that if the tooth was cut or damaged during removal, then there was less chance of a recordable hypoplasia being damaged or obscured. Once the lingual jaw bone had been removed, the teeth were carefully extracted.

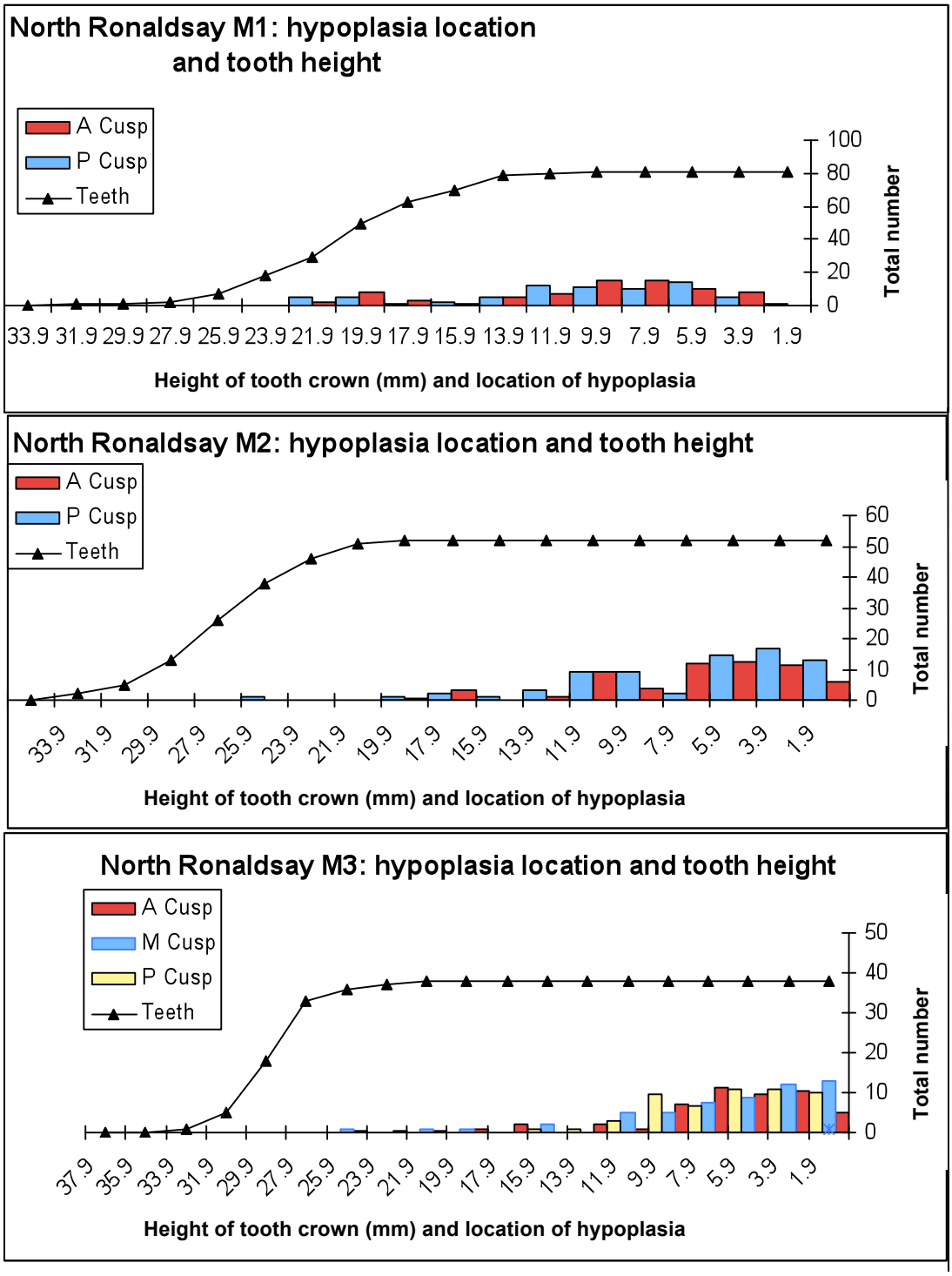

Figure 4.5: The location and frequency of enamel hypoplasia on the anterior (A), middle (M) and posterior (P) cusps, of a population of modern North Ronaldsay sheep. The X axis shows the position of enamel hypoplasia defects along the length of the tooth crown divided into 2mm categories. The Y axis shows the frequency of enamel hypoplasias. The line denoted by triangles shows the total number of teeth available for study in each 2 mm height category. This clearly shows that dental wear, while removing the upper portion of the tooth crown does not effect the recording of enamel hypoplasia location.

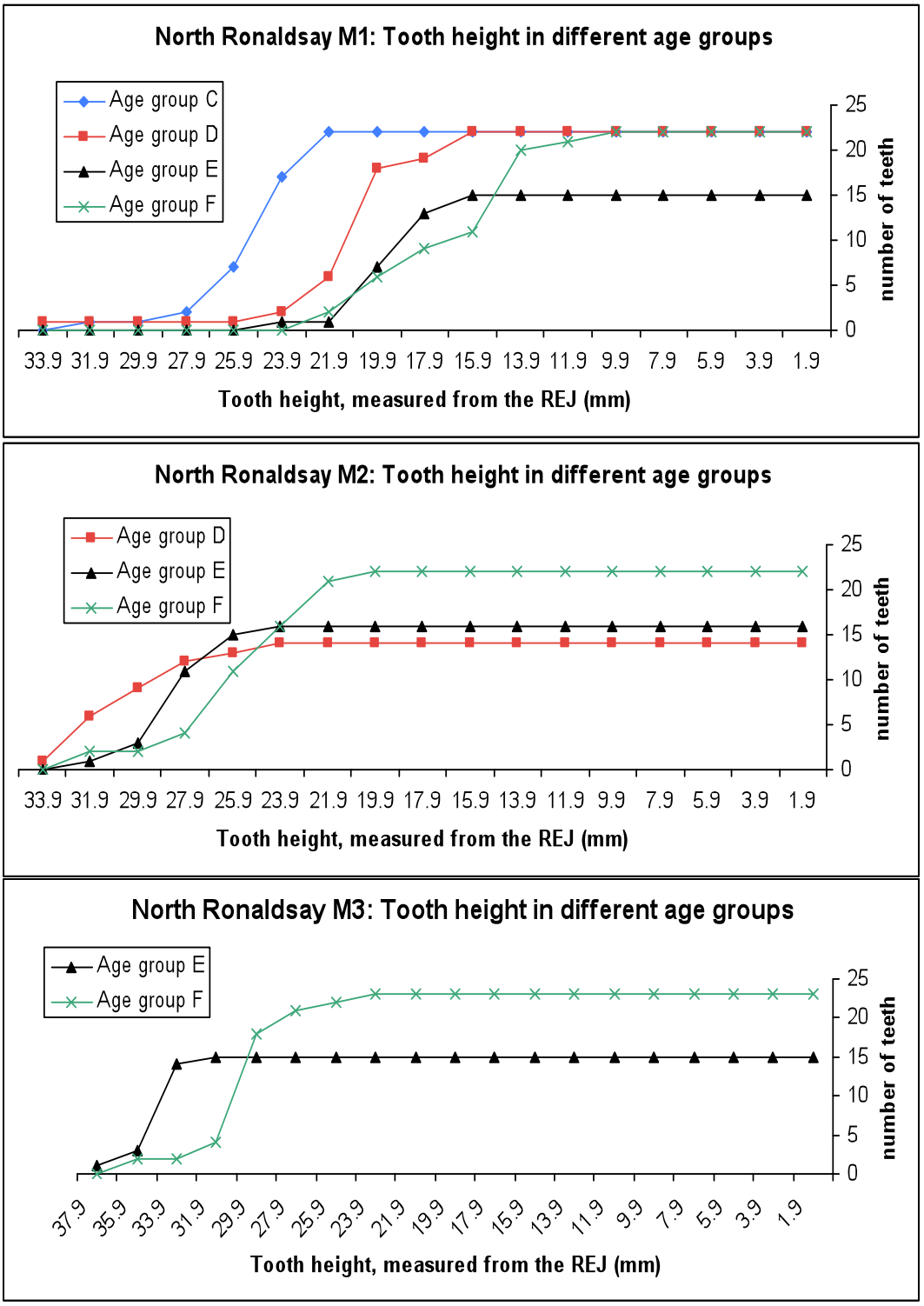

Figure 4.6: The effect of tooth wear on crown height in the age groups recorded in the North Ronaldsay population. Only complete teeth are recorded, explaining the absence of some age groups in the later forming teeth. The X axis represents the length of the tooth crown divided into 2mm categories. The Y axis shows the total number of teeth available for study in each 2 mm category.

Figure 4.7: A caprine mandible with the bone removed over the three permanent molars.

4.3 Separating sheep and goats

In some of the archaeological populations studied in the following chapters there is the possibility of both sheep and goats being present. It was considered important to separate these two species as they potentially may have very different developmental signatures due to differences in husbandry and feeding practises. Work on modern populations of Kenyan sheep and goats by Balasse & Ambrose (2005b) tested and refined morphological criteria for sheep/goat separation developed and described by Payne, 1985; Helmer, 2000 and Halstead, et al. 2002. Using known sheep and goats collected in the field, Balasse & Ambrose (2005b) identified two key morphological differences in sheep and goat molars, related to point M3.6 highlighted by Halstead, et al. (2002). These key traits are located on the anterior surface of the molars and are shown in Figure 4.8.

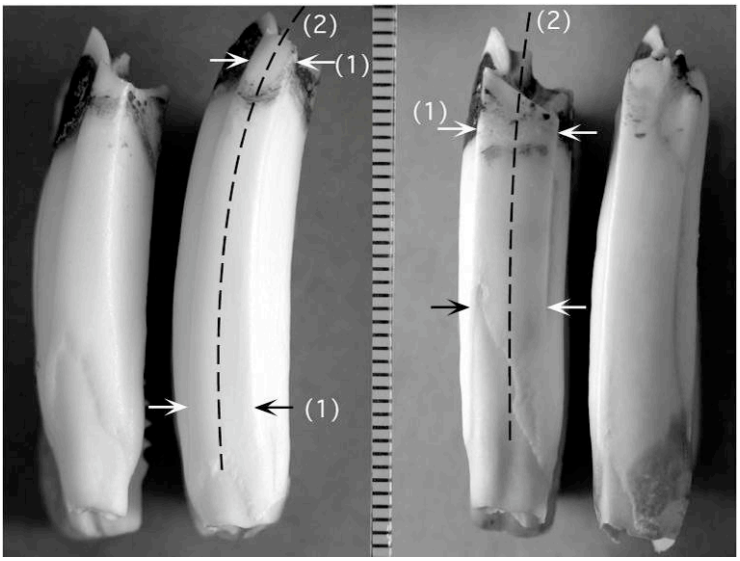

Figure 4.8 : The major morphological differences between goats (shown on the left) and sheep (shown on the right). Key trait 1: the anterior tooth surface in goats narrows dramatically from the wide cervical end to the narrow occlusal end. In sheep the anterior surface retains its width for the height of the tooth. Key trait 2: in goats the anterior tooth surface follows a significant curvature where as the sheep is much more upright and vertical (From Balasse & Ambrose, 2005b: 695).

Using these new morphological criteria, Balasse & Ambrose (2005b) were able to separate the unidentified modern Kenyan mandible specimens to individual species. This was then further tested by the application of isotopic analysis to both the identified and the unidentified individuals. As sheep and goats consume different food groups due to their different feeding methods (sheep by grazing, goats by browsing) they were expected to have different dietary isotopic signatures. This isotopic work on both the known and unknown individuals supported the initial morphological separation into sheep and goats (Balasse & Ambrose, 2005b). All sheep and goat separations in the archaeological Kenyan material (discussed in Chapter 6) are based on this methodology combined with the previous methodologies developed by Payne, 1985; Helmer, 2000, Halstead, et al. 2002. Based on the evidence from the modern material, the method developed by Balasse & Ambrose (2005b) appears to provide an accurate method of separating these two species in material from Kenya.

4.4 Recording enamel hypoplasia in caprines

The methods used in this research are based primarily upon the methodology created by Dobney & Ervynck (1998) and adapted to account for the various problems associated with high-crowned species. As this research aims to investigate if and how enamel hypoplasia can be used to study animal husbandry in sheep in the past, it was important to remove any potential bias from the datasets. For this reason all teeth that were included in this study had to have both buccal cusps present and undamaged. Teeth which had broken or damaged cusps, which prevented both cusps from being fully recorded, were not included in this study.

4.4.1 Which teeth?

Only mandibular teeth were included in this study. The exclusion of maxillary teeth is justified to avoid duplication of data. As discussed in previous chapters, any physiological or environmental stress event should theoretically be recorded equally in all teeth developing at the time of its occurrence. Mandibular teeth were selected over maxillary teeth on the basis that complete mandibular rows are more likely to survive in the archaeological record than maxillary tooth rows (Dobney & Ervynck, 1998). Also there is considerably more data to support the accurate aging and assessment of mandibular teeth than is available for maxillary teeth (e.g. Silver, 1970; Payne, 1973).

Only the three permanent molars are included in this study. In order to prevent multiple recording of the same stress events, only one of any synchronously developing teeth needs to be recorded. As the three permanent molars sequentially cover all of the developmental periods of an animals life from birth to the end of the period of dental development, the inclusion of other teeth in this study was deemed unnecessary. Deciduous teeth were excluded from the study as preliminary analysis of one of the modern populations studied (North Ronaldsay), as well as work by Arbuckle (in press, discussed in section 4.1) on the presence and location of hypoplasia on sheep teeth, demonstrated that deciduous teeth show very little

evidence of hypoplasia. Arbuckle found defects in between 0-8.4% of all deciduous teeth compared with 13-19% of first molars, 20-23% of second molars and 30-53% of third molars. There are several reasons why the deciduous teeth may not show hypoplastic defects. The first is that these teeth develop very rapidly, limiting the time period for stress events to cause enamel defects and then manifest them on the tooth crown surface (see previous chapter). The second is that the deciduous teeth form before birth and consequently the foetus is buffered from external stresses from the mother.

4.4.2 Which age categories?

Mandibles from animals in Payne's (1973) age classes A (0-2 months) and B (2-6 months) were not used for several reasons. Sheep are born with all their deciduous teeth fully formed and the first molar crown partially developed. However, mineralization is not completed in the upper part of the first molar until age stage C (6-12 months). Un-mineralised enamel is very pitted and porous in appearance, rendering the accurate identification of any LEH in these un-mineralised areas very difficult (Figure 4.9). Mandibles from age class G (4-6 years) onwards were also not used, if statistically valid sample sizes could be gained from recording mandible in categories C to F (discussed above in section 4.2.2). This was done to reduce the possibility that dental wear would remove hypoplasia in the occlusal half of the crown, even though, as discussed above, it has been demonstrated that enamel defects occur exceptionally rarely in the occlusal half of the tooth crown.

Figure 4.9: An incomplete first molar from North Ronaldsay (NR 84.2). The cervical half of the tooth crown is un-mineralised and clearly shows the pitted porous appearance of un-mineralised enamel.

4.4.3 Left or right?

The decision to focus on either left or right sided specimens is one which is highly variable between assemblages. A range of factors affect this decision, including the taphonomic preservation of the remains and the type of deposition, for example complete skulls. However, as in most archaeological assemblages, the contexts included in this study contained mainly mixed butchery refuse, as such the chances of being able to unite left and right sides are limited. Consequently for the archaeological remains both left and right mandibular rows and teeth were analysed. In the modern samples such as that from the island of Hoy, Orkney where complete

individuals were available for study, only one side of each mandible was recorded, the side selected again was dependent on various factors, including the presence of any pathological defects which needed to be preserved for future research and the presence of all three molars.

4.4.4 Sorting and cleaning samples

The mandibles and teeth from each sample were all numbered and catalogued. Mandibles were then separated into age classes following Payne (1973). Once teeth had been extracted (as discussed above in section 4.2.2), they were then manually cleaned under running water for a few minutes using a toothbrush until the enamel surface was clearly visible and free of dirt. Visible coronal cementum was also removed if possible by gently scraping or flaking with sharp pointed tweezers or a dental probe. The teeth were then air dried overnight and placed in labelled bags, along with the jaw from which they were extracted and all the bone fragments produced during the extraction.

4.4.5 Which surface to record?

Arbuckle (in press) recorded hypoplasia on all tooth surfaces. However, preliminary research on the North Ronaldsay material revealed that enamel hypoplasia were both most common and most visible on the buccal surface and that where they did occur on the lingual surface, it was almost always in relation to a more visible defect on the buccal surface (Figure 4.10). Because of this result, it was decided to limit the hypoplasia recording to only the buccal aspects of each cusp, ensuring that the maximum amount of data was recorded while keeping the data-set manageable.

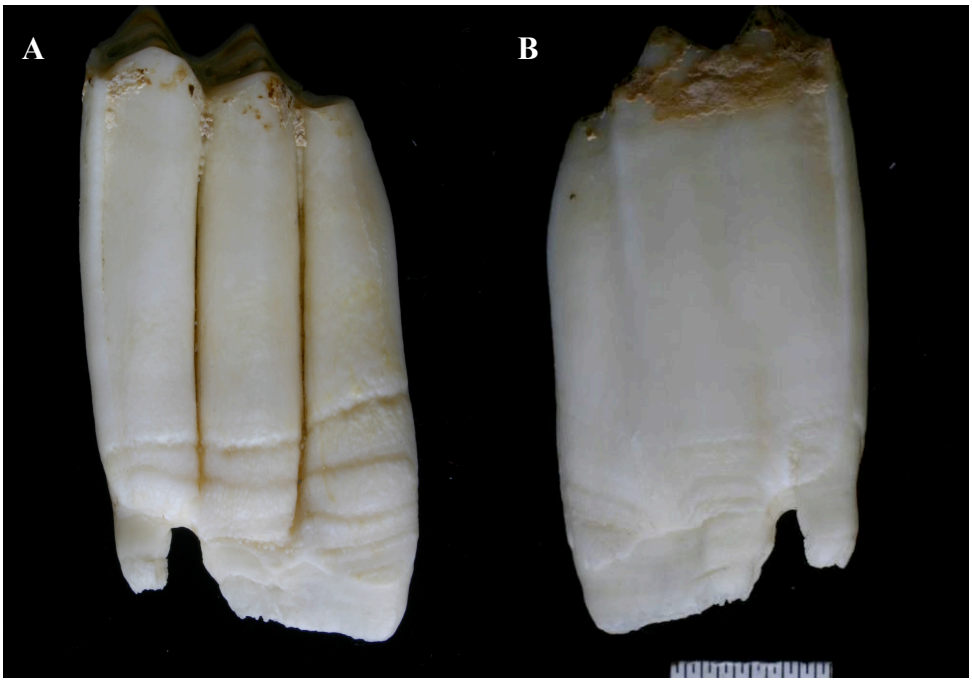

Figure 4.10: The buccal (A) and lingual (B) views of a right third molar from North Ronaldsay (NR 84.126). Enamel defects are replicated on both aspects but clearly more visible on the buccal surface.

4.4.6 Defect types

Teeth were viewed under a strong oblique light to allow the enamel hypoplasia to be seen more clearly. As the enamel hypoplasia most commonly took the form of a groove running horizontally across the tooth surface or pits in the enamel, the defects were revealed as enhanced shadows on the enamel surface when the light was shone vertically down or obliquely across the tooth surface. Once the defects had been located and positively identified, as neither simple discolouration nor taphonomic damage, they were recorded. Each hypoplasia was classified as a line, depression or pit; (Figure 4.11 and see Chapter 3 for detailed descriptions).

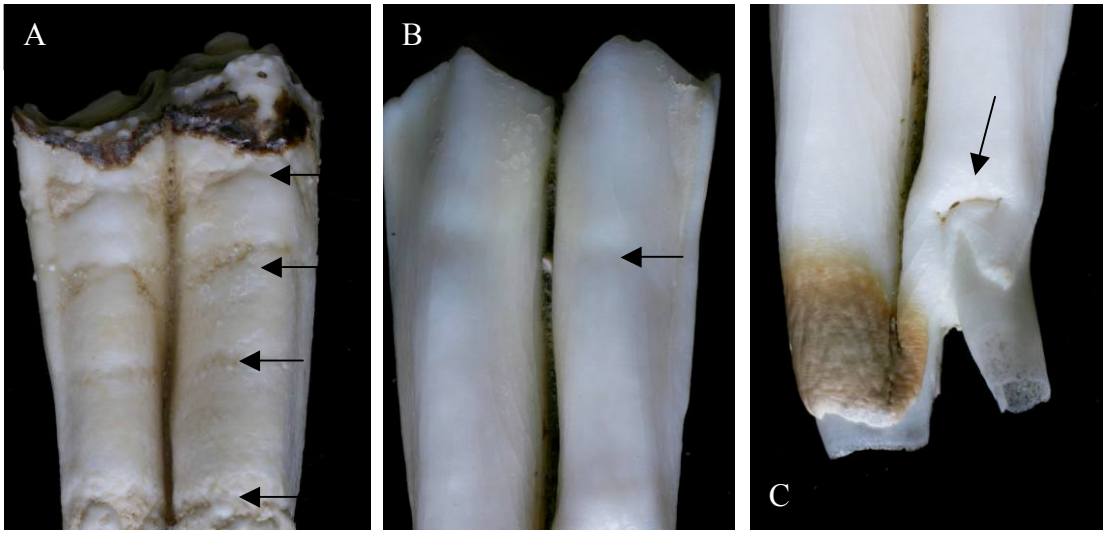

Figure 4.11: The different types of defect recorded, indicated by arrows (A = lines; B = depression; C = pit).

4.4.7 Defect severity

Severity scores were also given to all line type hypoplasias. This was only undertaken for line type hypoplasia defects as preliminary research indicated these were the most commonly occurring type of defect. The classification of line type defects and their severity scores are shown in Table 4.1. Photos of each category are shown in Figure 4.12.

Severity score	Classification of linear defects.
1	Defect is only visible using a strong directional light source.
2	Defect is just visible without the light source.
3	Defect is clearly visible without light source.
4	Defect is clearly visible, enamel is clearly missing, disrupted or very poorly mineralized (4a) and/or defect covers a large area (4b).

Table 4.1: The classification of the severity of linear defects.

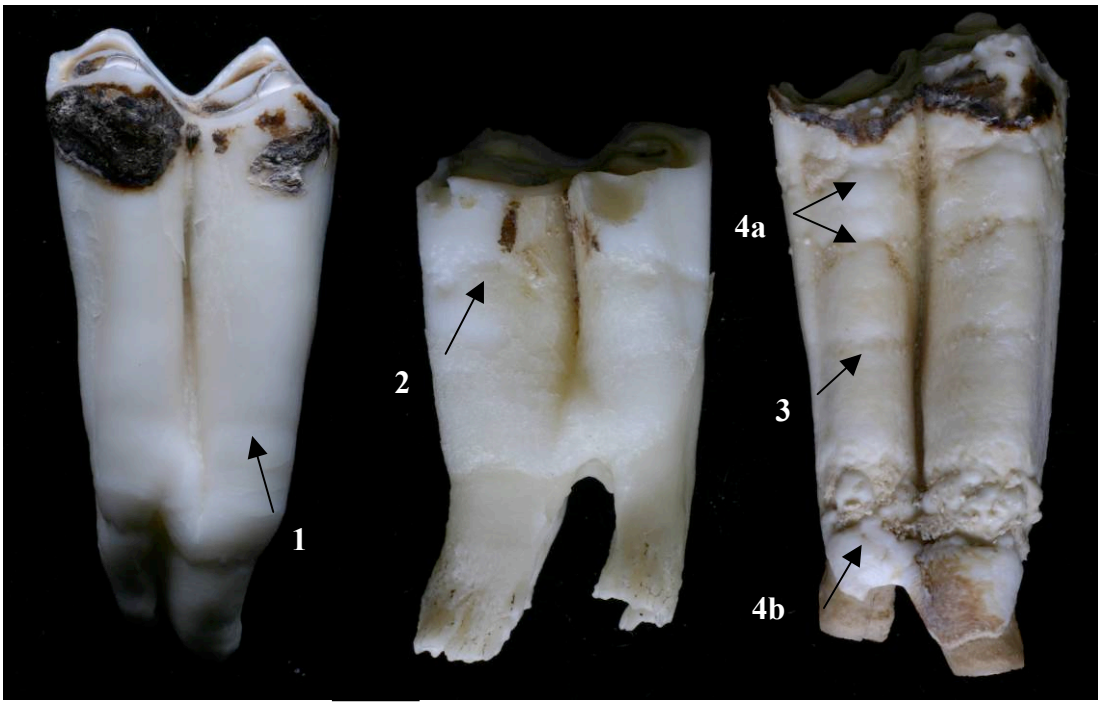

Figure 4.12: The severity scores of linear defects scored for severity. Arrows indicate the location of the defects and their severity score.

4.4.8 Measurements

Once undamaged teeth had been identified, sided, and aged according to Payne (1973) the maximum height of the tooth crown was recorded. Measurements were taken on the lingual surface from the groove between the tooth roots to the tip of the anterior cusp (see Figure 4.13). The groove between the roots provides a constant point on all teeth from which to measure, overcoming any problems associated with locating a consistent reference point on the variable REJ on which to locate a landmark. All measurements were taken to the nearest 0.1mm with digital callipers. The measurement of 'maximum tooth height' is essential in the reconstruction of dental chronologies as discussed below.

In teeth with fully developed crowns, the location of enamel hypoplasia was measured from the REJ vertically through the centre of each cusp, beginning with the anterior cusp (see Figure 4.13). In cases where the hypoplastic defect took the form

of a large pit, cluster of small pits or a wide groove, both the upper and lower points of the defect were measured. In teeth where the enamel extension had not quite finished but was clearly within a few millimetres of completion, the distance of the defect to the REJ was estimated, allowing the tooth to be recorded as a complete crown.

Incomplete teeth were also recorded as part of this study. This was done to further investigate dental wear and the occurrence of enamel hypoplasia. In preliminary studies incomplete teeth very rarely showed enamel defects, supporting the suggestion previously discussed, that dental wear will not significantly bias the recording of enamel defects to the lower half of the tooth. For example in the North Ronaldsay population, just 9% of incomplete teeth showed evidence of enamel defects. In incomplete crowns, enamel defects were recorded by measuring down from the buccal tip of the crown along the centre of each cusp (starting with the anterior cusp) to the hypoplastic defect (See Figure 4.13) Again, if the hypoplasia took the form of a large pit, cluster of small pits or a wide groove both the upper and lower points of the hypoplasia were measured. However, in almost all cases very few incomplete teeth showed evidence of enamel hypoplasia. Ultimately, incomplete teeth were excluded from the bulk of the hypoplasia analysis due to the very limited number of defects recorded on incomplete crowns, as well as the problems associated with linking two data sets (complete teeth and incomplete teeth) together in a coherent chronology (details on the development of the dental chronology and the difficulties of linking the enamel hypoplasia to it are discussed in sections 4.5.1 and 4.5.2).

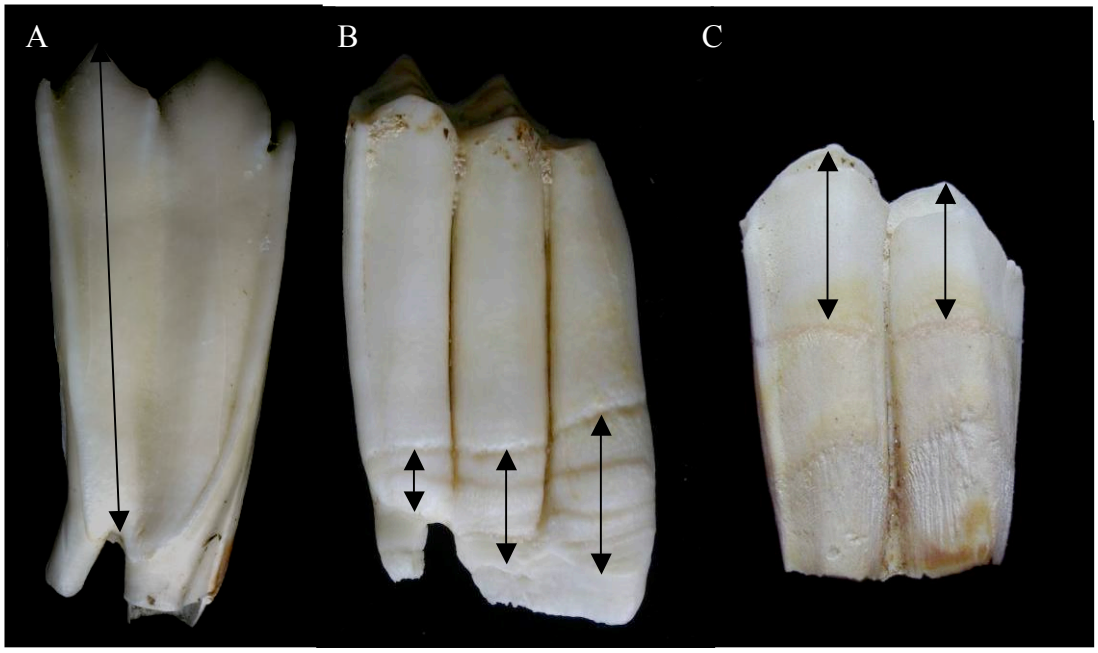

Figure 4.13: A) the measurement of the maximum height of the tooth crown ; B) the measurement of hypoplastic defects on complete tooth crowns and C) the measurement of hypoplastic defects on incomplete crowns.

4.5 Developing dental chronologies

Perhaps one of the most interesting aspects of enamel hypoplasia is its chronological formation and the potential for that chronology to be reconstructed in relation to dental development and linked to known stress events. In humans there have been multiple methods applied to the chronological study of physiological stress through enamel hypoplasia, as outlined and discussed in the previous chapter. This section will discuss the development of a dental chronology for caprine teeth and how this chronology influences the analysis of enamel hypoplasia in caprines. There are two key aspects to be considered when looking at the development of dental chronologies for the study of enamel hypoplasia. The first is the period of growth for each tooth, in relation to the age of the animal; for example, the age at which the second molar begins to form and at what age the crown is completed. The second is the rate of enamel development within the tooths formation period.

4.5.1 Dental growth in caprines

In order for enamel hypoplasia to be studied in relation to physiological and seasonal factors, it must be related to the age of the animal at the time of defect formation. It is therefore vital that the period of formation for the three molars in caprines be documented. While there are many papers published on the eruption rates of caprine teeth, there is very limited published data available on the periods of tooth formation in caprine populations. Where they exist, papers providing tooth development rates for caprines are principally focused on the incisor teeth or the very earliest stages of dental development such as the cap, bud and bell stages (for example Thurley, 1985 & Witter & Míšek, 1999). A paper by Milhaud and Nezit, (1991) studied the development rates of molars in 48 south Pre-Alps ewes. These animals lived under optimum nutritional conditions, potentially leading to faster rates of dental development, making them an unsuitable comparison to both archaeological samples and to the slow growing animals from the modern data sets studied in this research. A paper published by Weinreb & Sharav (1964) studied the development rates of unimproved Awassi sheep. The data provided by this paper and that provided by

Milhaud and Nezit, (1991) are summarised in Table 4.2 below. Unfortunately neither of these papers provides definitive dates for dental crown completion. Therefore, assumed crown completion dates, based on the data provided by these papers, are also shown in Table 4.2.Within the modern assemblages studied, there is one population of Shetland sheep from the Orkney island of Hoy, which has known age-at-death data. This population was also studied with regard to dental formation rates and the results are shown in Table 4.3. The data from both Weinreb & Sharav (1964) Milhaud and Nezit, (1991) and the modern Hoy population are then compared in Figure 4.14.

Tooth	Data from Weinreb & Sharav, 1964	Assumed period of crown development based on Weinreb & Sharav, 1964	Data from Milhaud and Nezit, 1991	Assumed period of crown development based on Milhaud and Nezit,1991
First Molar	•Crown ½ formed at birth •3-6 months 2/3 of crown formed •9 months after birth crown completed roots starting & tooth wear	Pre birth to 9 months	• Begin formation in utero •Erupts at 3 months •Root begins to form at 6-7 months	pre birth to 7 months
Second Molar	•3-6 months 1/3 crown formed •9 months - crown still forming •1 year - crown complete & erupting •1 ½ -2 years - little root & tooth wear	2 months to 12 months	• Begins formation 1 month after birth •Erupts at 9 months •Root begins to form at 11 – 12 months	1 month to 11 months
Third Molar	•1 year buds visible •1 ½ - 2 years crown almost complete •2 ½ - 3 year root formation	12 months to 25 months	• Begins formation at 9-10 months •Erupts at 18-24 months •Root begins to form	9 months to 21 months

Table 4.2: A summary of the dental development data given by Weinreb and Sharav (1964) and Milhaud and Nezit, (1991) and the assumed dates of crown completion based on the data from these papers.

Known Age at death	Payne Age	M1	M2	M3
8 months	C	Almost complete	Incomplete	Development not started
8 months	C	Crown complete	Incomplete	Development not started
10 months	C	Crown complete	Incomplete	Development not started
10 months	C	Crown complete	Incomplete	Development not started
11 months	C	Crown complete	Incomplete	Development not started
15 months	D	Crown complete	Almost complete	2 buds present
15 months	D	Crown complete	Almost complete	1 bud present
18 months	D	Crown complete	Crown complete	Incomplete
18 months	D	Crown complete	Crown complete	Incomplete
20 months	D	Crown complete	Crown complete	Incomplete
20 months	D	Crown complete	Crown complete	Incomplete
21 months	D	Crown complete	Crown complete	Incomplete
23 months	D	Crown complete	Crown complete	Incomplete
27 months	E	Crown complete	Crown complete	Incomplete
29 months	E	Crown complete	Crown complete	Incomplete
29 months	F	Crown complete	Crown complete	Complete on A & M cusps but not P
31 months	E	Crown complete	Crown complete	Complete
31 months	E	Crown complete	Crown complete	Complete
31 months	E	Crown complete	Crown complete	Complete
31 months	E	Crown complete	Crown complete	Complete
32 months	E	Crown complete	Crown complete	Complete
32 months	E	Crown complete	Crown complete	Complete
34 months	E	Crown complete	Crown complete	Incomplete
35 months	E	Crown complete	Crown complete	Incomplete
35 months	F	Crown complete	Crown complete	Complete
36 months	E	Crown complete	Crown complete	Complete

Table 4.3: The dental development data from the known age-at-death recent Shetland sheep specimens from Hoy, Orkney.

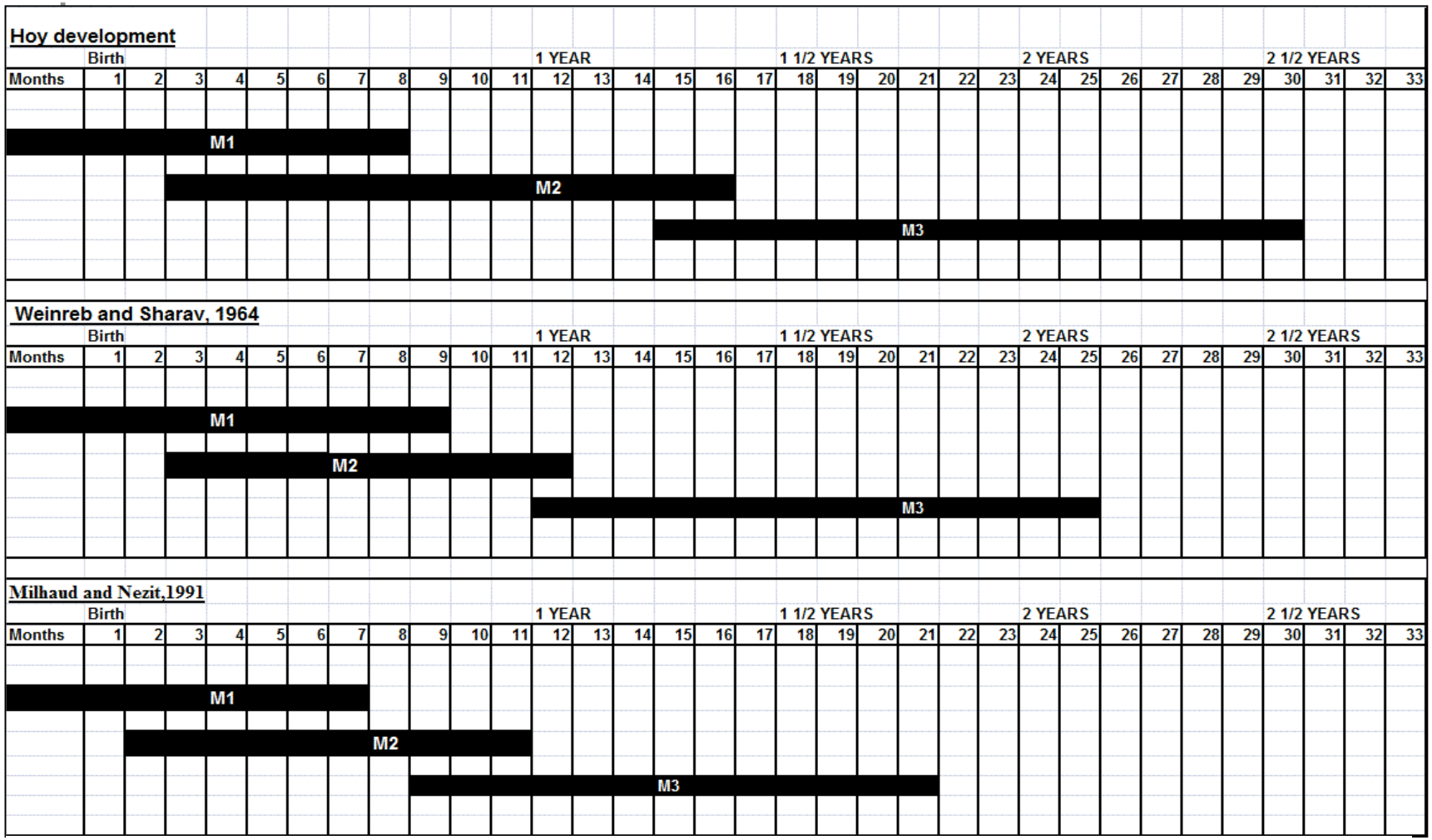

Figure 4.13 The differences in recorded developmental rates between the modern material from Hoy and the data published by Weinreb & Sharav, 1964 and Milhaud and Nezit, 1991 . The periods of purported/observed dental development for each molar are shown in black; months after birth are marked along the top of each graph. M1 = first molar, M2 = second molar, M3 = third molar.

Figure 4.14 reveals clear differences between the published caprine dental development rates and the developmental rates observed in the modern Hoy assemblage studied as part of this research. There are several possible explanations for this variation. As previously outlined, the paper by Milhaud and Nezit, (1991) studied animals living under optimum nutritional conditions, which potentially explains the very fast development rates seen in this population. The study by Weinreb and Sharav (1964) was carried out on fat tailed Awassi sheep. This is a traditional breed from the Middle East (Epstein 1985) which could have very different dental development rates from the Shetland sheep breed. However, a more likely explanation for the apparently markedly earlier crown completion times could be attributed to a lack of clarity about what was actually recorded. The paper by Weinreb and Sharav (1964) gives no description of which surface of the teeth were recorded, or by what criteria a tooth crown was classed as complete. As the buccal and lingual surfaces of caprine teeth complete development at different times, it is possible that Weinreb and Sharav were recording crown completion and root development on the lingual surface of the tooth, which completes development before the buccal surface, explaining the early completion times on the second and third molars. As this study focuses on enamel hypoplasia recorded on the buccal surface (for the reasons discussed above) it was important to understand the developmental chronology for this surface and not the lingual surface. For this reason, the dental chronology model developed from the modern Hoy assemblage (shown in Figure 4.14) is used throughout this study as the key model for dental development rates in caprines.

4.5.2 Enamel growth rates in caprines

Once the chronology for dental development was established, it was important to investigate the growth rates of enamel within that chronological framework. The formation of enamel hypoplasia is inextricably linked to the incremental growth of enamel, as previously discussed in Chapter 2. As discussed in detail in Chapter 3, early studies on developmental chronologies of enamel have often assumed it follows a linear pattern, with enamel being produced at a constant rate throughout the period of crown development. More recent studies into human teeth have demonstrated that

this is not the case (Skinner & Goodman, 1992; Goodman & Song, 1990; King, et al. 2002). It has been argued that this variation in enamel development in humans has little affected the study of enamel hypoplasia (Martin, et al. 2008, see Chapter 3). However, given the exceptionally long development periods of caprine teeth it was felt that it was important to establish any variation in enamel growth rates. Potentially the long period of dental development could enhance any variation in enamel growth rates, leading to enamel defects being incorrectly related to various seasonal events.

Histological analysis was carried out to investigate enamel growth rates in caprines. As discussed in Chapter 2, teeth develop in incremental layers known as the striae of Retzius. These develop at regular intervals during the course of tooth formation. By looking at the number of incremental striae occurring in a section of dental enamel it is therefore possible to suggest how long it took that section of enamel to develop relative to other sections of enamel. A thin section cut through a caprine third molar is shown in Figure 4.15. This figure clearly demonstrates that the occlusal half develops much faster than the cervical half of the tooth crown. This is clearly indicated by the increasing number of incremental lines per micron of dental enamel in the cervical half of the tooth crown. This allows a relative chronology of dental growth rates to be developed, with the occlusal half of the tooth crown growing at approximately twice the speed of the cervical half.

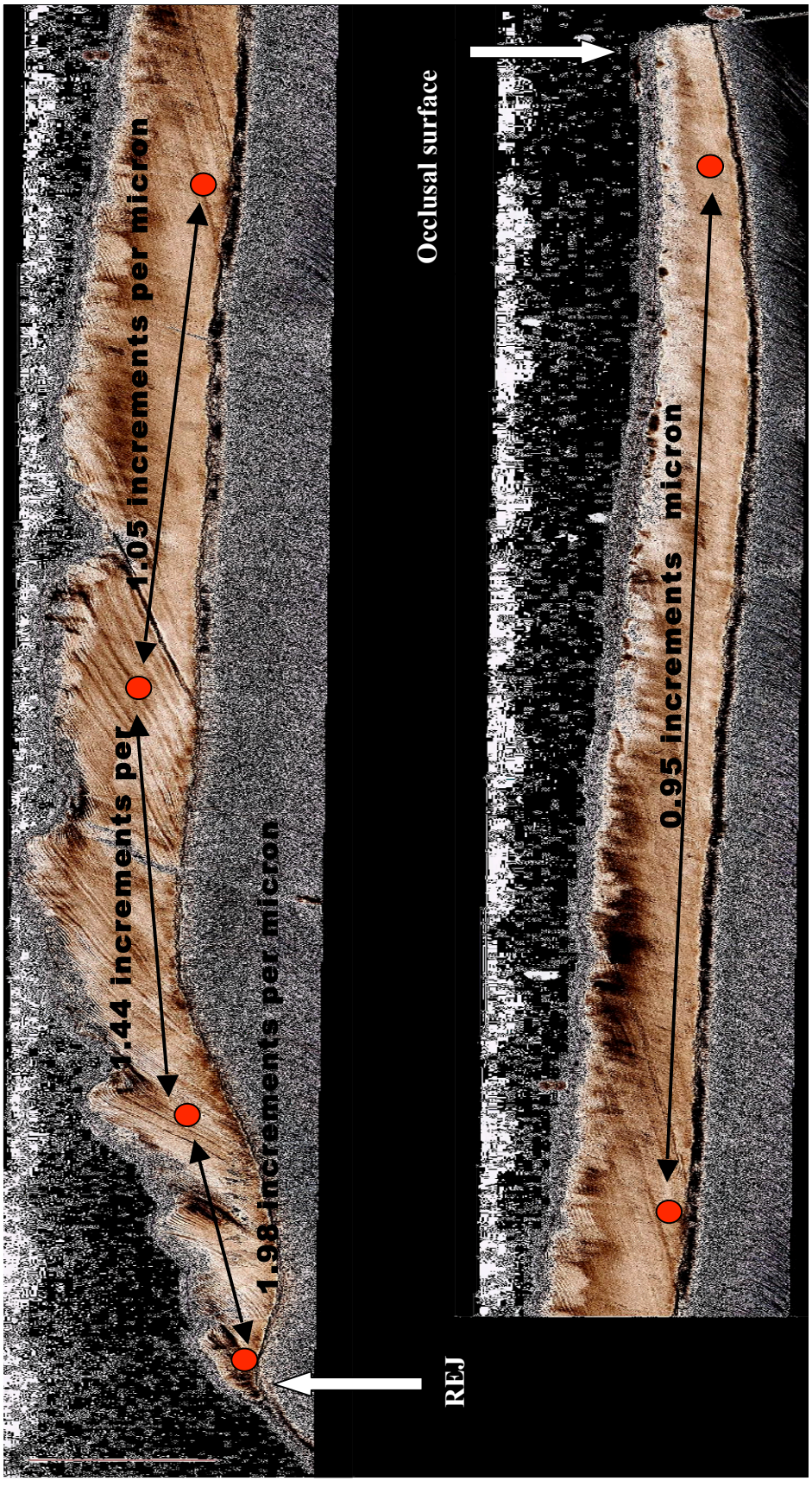

Figure 4.14: Thin section through a caprine third molar. The two images shown are of the same tooth, the lower image is of the occlusal half and the upper image is of the cervical half. Red dots mark the points from which the enamel increments were counted.

4.5.3 Problems with dental chronologies in high crowned species

Dental wear

Potentially, one of the most serious problems for the successful linking of enamel defects to dental chronologies in high-crowned species is caused by dental wear. In low-crowned species the teeth erupt into the mouth fully formed. This enables complete, unworn crowns to be recovered from these low-crowned species. These unworn crowns provide two fixed points on each tooth: the unworn tip of the crown and the root-enamel junction (REJ) allowing a measurement of the total unworn crown height to be recorded. When this is combined with dental development rates, it can be used to create estimations of the monthly growth rates of enamel. This allows a chronology of dental development to be created, i.e. the rate of enamel growth per month. This chronology of dental development can then be related to the location of the enamel hypoplasia on the tooth crown and consequently the age of the animal at the time of development of the hypoplastic defect. Animals with high crowns such as sheep, goat and cattle pose a problem as their teeth continue to grow after the tooth has come into wear. This means that a complete, unworn crown is never available for these species, rendering the development of dental chronologies difficult, and leading to problems when trying to relate the location of dental defects to events which may have caused them.

Variation in tooth size

Obviously, variation in the size of tooth crowns between populations can also potentially seriously affect the comparative relative chronology of enamel defects. This is especially true if larger teeth take longer to develop, as opposed to just developing faster. Unlike other species, caprine teeth are not sexually dimorphic and so sex differences are not considered to be issues for this research. However, potential differences in size between sheep and goat populations may well affect the data. The problem of dental wear as discussed above adds an extra complication to the problems of tooth size. For example, if a young population of sheep is compared to an old population of goats, the advanced dental wear of the goats will produce

smaller crown heights indicating a smaller tooth size, even if the teeth of both species were the same size to begin with.

4.5.4 Overcoming the problems of dental chronologies in high crowned species

Being able to explore the links between enamel defects and seasonal and physiological events is essential for interpreting patterns in the datasets. Variation in tooth size and dental wear between populations can potentially cause problems in the interpretation of the location of enamel defects within chronologies of dental development.

Dental wear

In high-crowned species the long development rates and dental wear mean that there are never complete unworn crowns available for study. This means that in complete molar crowns there is only ever the REJ available as a fixed reference point. This point marks the end of the development of the enamel tooth crown. The lack of a complete unworn crown means that the exact rates of enamel growth per week cannot be calculated. Therefore a different approach to relating the location of defects to the time period in which they occurred has to be taken. As previously discussed, Arbuckle (in press) attempts to overcome this problem by adding an arbitrary 33% of the crown height onto the measurements of the tooth crown, assuming that 33% is lost due to tooth wear. However, as discussed above in section 4.1, this is far from ideal, given the variation in dental wear that can occur within populations and age groups.

Dobney and Ervynck (1998) overcame the potential problem of variation in tooth size between populations by using the relative height of the defects compared to the maximum height of the unworn tooth crown. They go on to say that if no complete teeth were present, animals with limited tooth wear could also be used to provide

maximum height measurements. This research uses a very similar method to deal with the potential problem of tooth wear. While there are never complete, unworn crowns available for study in caprine populations, there are complete crowns with very limited wear. This research takes advantage of that fact, as discussed above, that the upper part of the tooth crown develops very quickly and rarely contains hypoplastic defects in the enamel. The height of the largest, complete, least worn crown from each molar group (M1, M2, M3), in each population is selected and this is then used as the baseline onto which dental defects are plotted. This baseline can then be fitted into a developmental chronology for sheep teeth as discussed in section 4.5.1. Complete teeth were selected with Payne (1973) wear stages of between 3 and 5. This ensures that only a few millimeters of tooth crown are missing (for example at Payne wear stage 5 on the second molar, approximately 6 millimeters of the tooth crown is missing). Once the teeth are plotted into the developmental chronology, the variation of a few millimetres of enamel becomes irrelevant, as it is broad time scale patterns that are being investigated

Variation in tooth size

Obviously, the margin of error potentially caused by variation in tooth size between populations is reduced if the sample is homogeneous. This is why it is essential that a balance of old and young individuals are present in each population studied. It is also for this reason that specimens of sheep and goat within a sample need to be carefully identified, separated and checked for variation in tooth size. The possibility of different breeds being present within archaeological populations is another potential issue that can be partially addressed through by biometric analysis checking for variation in tooth size within dental wear stages. Based on the assumption that teeth grow at the same rates, regardless of tooth size (i.e. the same percentage of the tooth crown is developed within the same time frame), the method discussed above for dealing with dental wear also combats any issues of variation in tooth size between populations by scaling the maximum tooth size from each population to fit into the chronology of dental development.

4.6 Data Analysis

4.6.1 Plotting enamel hypoplasia against new caprine dental chronologies

In order to allow patterns in the location of enamel defects to be revealed, defects were plotted using histograms with ranges of 2 millimetre intervals. The use of 2 millimetre categories helped to smooth the data, removing any anomalous results, while retaining a high degree of resolution. The results were further smoothed using running means, allowing underlying trends in the data to become more clearly visible. In order to allow data-sets to be directly compared, each was converted to relative frequencies.

The discovery that caprine dental development rates are not linear along the tooth crown (as discussed in section 4.5.2 above) meant that the graphs had to be adjusted to reflect this. The histological analysis carried out demonstrated that the occlusal half of the tooth crown develops at approximately twice the speed of the cervical half of the crown. Consequently, enamel defects in the occlusal half of the crown were plotted in 4 millimetre groups and enamel defects in the cervical half of the crown were plotted in 2 millimetre groups. The half-way division was calculated from the maximum height of the tooth crown for each molar and each population. When these results are placed within a chronology of dental development, the occlusal half of the tooth represents approximately 25% of the development time, while the cervical half of the tooth is allocated the remaining 75%. Although this is clearly a relatively crude adjustment, finer level adjustments are not considered necessary. As discussed above, it is the broad time scale patterns that are being studied and more detailed adjustments will have little effect on the wider patterns produced.

4.7 Summary and future work

4.7.1 Problems and solutions to recording enamel hypoplasia in caprines

As discussed, there are several key problems which potentially can affect the recording and interpretation of enamel hypoplasia in caprine teeth. These are: coronal cementum, dental wear and tooth length. Coronal cementum has been demonstrated microscopically to affect all caprine teeth, regardless of macroscopic appearance. Its presence over all teeth means that within all populations there will be a consistent underscoring of the severity of enamel defects and a consistent number of defects that will be obscured completely by coronal cementum. While this research has not 'solved' the problem of coronal cementum it has demonstrated that it will affect all populations recorded equally and therefore will not be a biasing factor in this research.

It was thought that dental wear could pose serious problems to the recording of enamel defects in the upper portions of the tooth crown. However, this research has demonstrated that dental wear actually removes a relatively small portion of the tooth crown in the four main Payne (1973) age categories being studied. It has also been demonstrated that enamel hypoplasias very rarely occur in the occlusal portion of the tooth crown. Consequently, as long as there is roughly equal representation of young and old individuals in the population studied, dental wear will not pose a serious biasing problem to the recording of enamel defects. The long length of teeth in high crowned species poses a significant problem as most of the tooth is buried within the alveolar bone in complete mandible rows and isolated teeth cause problems with the separation of first and second molars. This is overcome by the careful extraction of teeth from complete mandibular rows.

4.7.2 Recording defects

This chapter has outlined a methodology for the recording of enamel hypoplasia in high crowned species based on previous methodologies created by Dobney &

Ervynck (1998). This method records only the buccal surface of the mandibular permanent molars. Three types of defects are identified and recorded: lines, pits and depression. Linear type defects are also scored for severity.

4.7.3 Developmental chronologies

There is a lack of published material relating to the developmental rates of molars in caprines. The two papers available give markedly different dental development rates to those seen in the modern assemblages studied from Hoy. The paper by Milhaud and Nezit, (1991) studied animals kept under optimum nutritional conditions possibly resulting in the rapid development rates seen in this population. The paper by Weinreb & Sharave, (1964) provides information on development rates, but is vague about what was recorded and it is suggested that the recording of different tooth surfaces may be responsible for the variation seen in development rates. Histological analysis has been used to create a relative chronology for enamel growth within caprine molars and this has demonstrated that the occlusal half of the tooth develops at approximately twice the rate of the cervical half of the tooth.

4.7.4 Data Analysis

The problems of tooth wear and tooth size are overcome by using the largest, complete, least worn tooth from each population as a baseline onto which the location of enamel hypoplasia can be plotted. This can then be scaled into the chronology of dental development in caprines. By plotting the data as relative frequencies the data can be compared between populations. Running means smooth the data, removing irrelevant information and allowing the underlying trends to be clearly visible. The graphs are adjusted for non-linear growth rates by altering the width of the categories used to create the histograms of enamel hypoplasia. Four millimetre categories are used in the occlusal half of the tooth crown and two millimetre categories are used in the cervical half of the tooth crown. Subsequently, when the graphs are plotted within the dental growth development models, the faster development of the occlusal half is reflected in its allocation of 25% of the

development time compared to the remaining 75% which is allocated to the development of the cervical half of the crown.

4.7.5 Future work

Clearly there is a need for more research into dental development rates in caprine populations. Modern populations, which have known age-at-death, need to be analysed from different breeds and regions. This will allow a better picture of the variation in dental development in caprine populations to be created, testing possible differences between traditional, slow developing breeds and improved, fast-growing breeds, as well as exploring differences in developmental rates between geographic areas. The continued histological analysis investigating enamel development rates is also essential. This could be used to produce a much more detailed understanding of the relative variations in growth rates down the tooth crown as absolute chronologies of crown growth.

5 Modern and archaeological caprines from Orkney

Each of the following three chapters applies the methodology developed in the previous chapter (Chapter 4) to geographically specific caprine populations. Each of these chapters investigates the application of the methodological approach and develops the interpretation and understanding of enamel hypoplasia in modern and archaeological caprine populations. The first of these three case studies involves the study of enamel hypoplasia in two modern sheep populations from the Orkney Islands of North Ronaldsay and Hoy and one archaeological population from the mainland Neolithic site of Skara Brae*. The two well-documented modern populations with their 'known life histories' are vital to developing an understanding of basic population based factors (such as diet and environmental conditions) which can affect enamel hypoplasia. By investigating known dietary and environmental differences in modern sheep populations and linking them to the occurrence and severity of enamel hypoplasia, a baseline understanding of the impact of diet and environment on the formation of enamel hypoplasia in caprines can be provisionally formed. This baseline will be used to interpret patterns of enamel hypoplasia in the sheep from Neolithic Skara Brae and will be developed in the following chapters to investigate broader interpretative issues such as past climate change. In this chapter three principal research themes are addressed: 1) identifying general levels of population stress relating to the baseline factors of diet and environment; 2) seasonality in terms of physiology and diet; and 3) the interpretative potential of recording enamel defect types and severity.

* The recording of the Skara Brae material was carried out in collaboration with Dr Marie Balasse and Dr Anne Tresset (Centre National de la Recherche Scientifique, Paris) as part of their ERC grant (2008-2013) SIANHE entitled 'Stable isotope investigations on the adaptations of Neolithic husbandry to the climatic and environmental settings of Europe'

5.1 An introduction to Orkney

The Orkney archipelago consists of a small cluster of islands located off the north coast of Scotland (Figure 5.1). Situated in the Gulf Stream, Orkney has a cool relatively stable climate with yearly temperatures ranging on average from 5 to 15 degrees centigrade. It is also one of the windiest places in the United Kingdom with gale force winds being recorded in low-lying regions on at least 30 days in every year. The strong storms and high winds which affect Orkney for much of the year carry salt from the sea which affects vegetation growth and development. Consequently animal husbandry is the major focus of the modern agricultural economy. While the focus in modern times is primarily on raising beef cattle, caprine remains are found in some of the earliest settlement sites on the islands such as Knap of Howar and Papa Westray, indicating that sheep have played a major part in the agricultural history of Orkney (http://www.orkneyjar.com/orkney/climate.htm & http://www.hie.co.uk/orkney/economy.html).

The long hard winters in the North Atlantic regions have always made the supply of fodder vital to the over-winter survival of domestic livestock. In some regions of the North Atlantic including Orkney, Shetland and Iceland, the use of seaweed as a source of fodder for mammals such as sheep, horses, cattle and pigs was, until recently, common. (Pringle, 1874; Williamson, 1948; Evans, 1957; Hallsson, 1964; Fenton, 1978). Seaweed foddering has all but died out in modern agricultural practices, although it appears to still occur occasionally in Orkney (Mainland, 2000). North Ronaldsay is one of the few remaining places where sheep survive on a diet consisting almost entirely of seaweed. In this chapter individuals from this population of seaweed eating sheep will be compared to another modern population of Shetland sheep raised on the southern Orkney island of South Walls, Hoy which grazed upon unimproved grassland and maritime heath. Data from both of these populations are then compared to archaeological caprine remains from the Neolithic

site of Skara Brae. The location of the Orkney Islands and the three sites to be included in this analysis are shown in Figure 5.1.

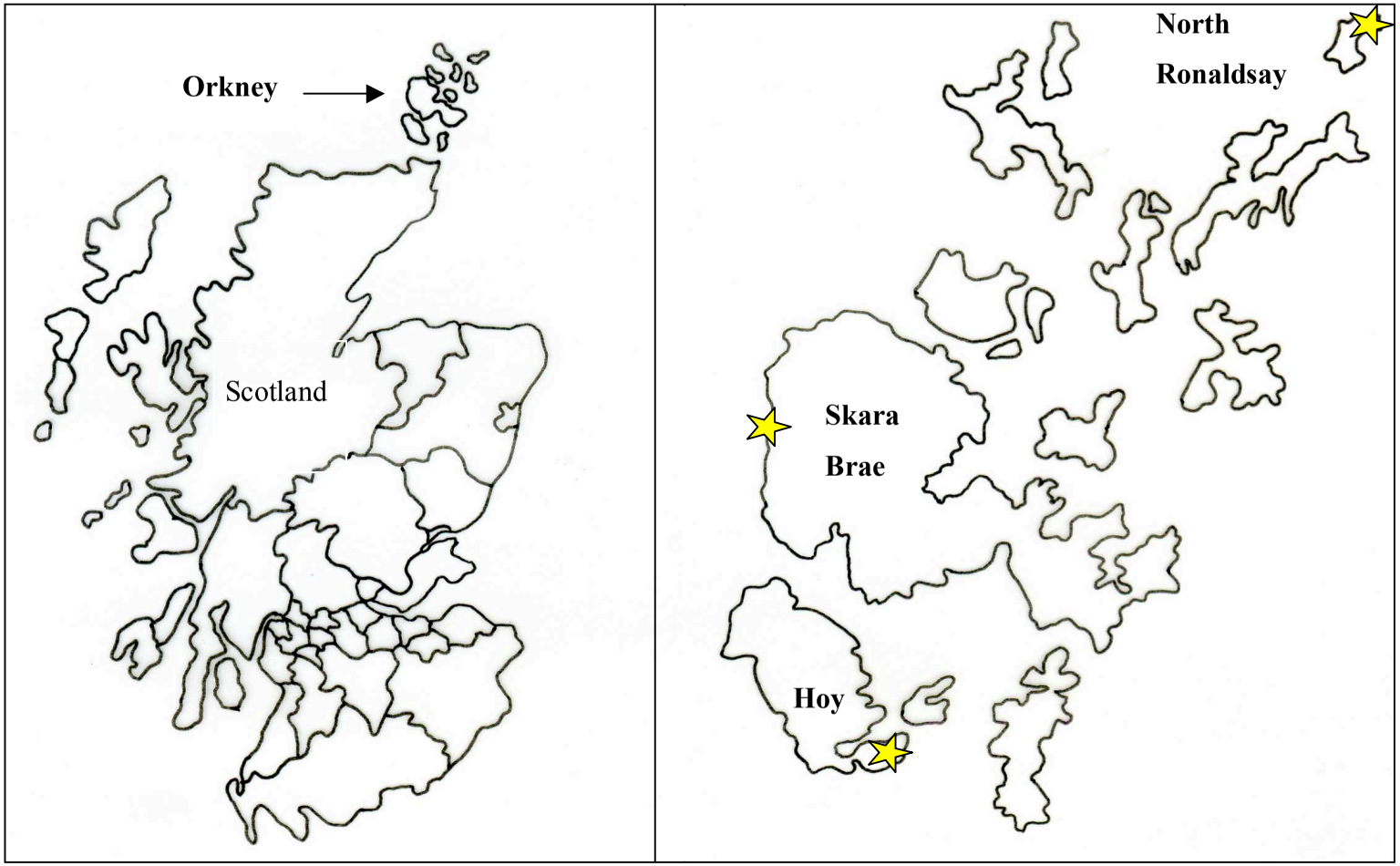

Figure 5.0: The location of the Orkney Islands including the locations of: Skara Brae, North Ronaldsay and South Walls, Hoy (After http://www.britainexpress.com/scotland/Orkney/Orkney-map.htm).

5.2 Background to the material

5.2.1 The North Ronaldsay sheep

Here in Rinansay

Sheep and ocean are one.

Ovine pulses beat

To the ebb and flow and slack.

They graze on wave-and-ocean plants.

Their flesh tastes of sea cabbage.

(Poem by George Mackay Brown, In Moberg & Mackay Brown, 1996: 22)

The North Ronaldsay sheep are a unique breed that feed almost entirely on seaweed. A large collection of mandibles and skulls from this breed, representing animals of all ages, was collected from the beaches around North Ronaldsay between 1983 and 1984 by Don Brothwell and in 1988 by Keith Dobney. As their remains were found on the beach it is likely that the animals collected died of natural causes.

The North Ronaldsay sheep are a small, short tailed, hardy breed, standing approximately 46 centimetres high at the shoulder and displaying a great variety of fleece colours ranging from white/cream through to black (MacLachlan, 1988). The North Ronaldsay sheep are a unique breed, which a century and a half ago were common on the islands of Orkney and Shetland but are now found principally on the most northerly of the Northern Isles of Orkney. The breed has uncertain origins; they are possibly indigenous to the area from the earliest agricultural times, or

alternatively they were introduced with the Norse colonists during medieval or more recent times (MacLachlan, 1988). A theory supported by the fact that they are quite similar in appearance to the Gotland breed (See Figure 5.1). It has also been suggested they may be closely related to the prehistoric Palustris or with rare breeds of Asian Arkhan sheep in Kazakhstan (MacLachlan, 1988).

Figure 5.1: A North Ronaldsay ram

(http://farfirst molar.static.flickr.com/229/468953541_e8f3b9120b.jpg?v=0)

The small population of native, semi-feral North Ronaldsay sheep were penned on the beach in 1832 when over population of the island led to a reorganisation of the land (http://www.caithness.org/history/articles/northronaldsaysheep2/backness.htm). A one and a half to two metre high stone dyke was constructed around the island keeping the sheep on the seaward side and preserving the central land for cattle grazing and arable cultivation (Mainland, 2000). There are approximately 193 hectares of rough pasture and about 265 hectares of inter-tidal ground at low water,

available to the sheep for grazing (MacLachlan, 1988). While there are patches of rough grass available for the animals to feed on, the majority of the land is rocky sand beach and the sheep preferentially feed on seaweed, in particular the brown kelp species (*Laminaria*) (Hansen, et al. 2003 see Figure 5.2).

Figure 5.2: North Ronaldsay sheep eating seaweed on the beach (Photo by P. Farmer, unpublished).

The animals feed on both fresh seaweed exposed at low tide and seaweed washed ashore. The only exception to this species' seaweed diet is during lambing season (April to May) when pregnant ewes are brought inside the dyke to give birth. The majority of lambs are born between the 3rd and 4th weeks of April and ewes stay inland feeding on grass until the lambing season is over when they are returned with their offspring to the beach (Fenton, 1969). The pregnant ewes are taken inland between April and August (Balasse, et al. 2005) to give birth and subsequently, in order to keep their milk yields high, as lack of seaweed in these summer months can

cause lactation to cease prematurely. Importantly for this study, and unlike normal terrestrial grazing sheep, the North Ronaldsay sheep are in their prime during winter, due to storms which pile seaweed 'on to the shore by the ton' (MacLachlan, 1988: 2). Locals observe that the sheep put on weight during these winter months and the North Ronaldsay mutton market closes in April for the summer months as the sheep lose quality from then onwards due to food shortages (Gourley, 2006).

Because of their diet of seaweed, these sheep have developed a series of specialised physiological adaptations, including the ability to cope with a diet high in salt and arsenic and with a very low copper bio-availability (Hall, et al. 1975; Orpin, et al. 1985; Haywood, et al. 2001; Hansen, et al. 2003; Simpson, et al. 2006). The sheep have also been forced to adapt their grazing habits to fit with the changing tides. Unlike normal terrestrial sheep that graze during the day and then ruminate at night, the North Ronaldsay sheep graze with the tides (twice every twenty four hours) and ruminate at high tide when their grazing areas are covered by water (MacLachlan, 1988).

Due to low amounts of bio–available copper found in seaweed, the North Ronaldsay sheep are especially sensitive to copper poisoning. Sheep are normally considered to be intolerant of high levels of dietary copper due to their inability to secrete copper in bile, leading to a build up of copper in the liver causing eventual copper poisoning (Simpson, et al. 2006). However, the North Ronaldsay sheep have been forced to develop mechanisms to maintain sufficient copper levels in their bodies, due to the abnormally low levels found in seaweed (Cu < 5 ppm). Unfortunately, this means that when the sheep are exposed to a copper sufficient diet (e.g. grass) they accumulate excessive amounts of copper in their bodies, leading to fatal toxicity (Simpson, et al. 2006).

5.2.2 The Hoy Sheep

The second modern population studied is from a flock of Shetland sheep kept on the island of South Walls, Hoy, in the south west of Orkney. Like the North Ronaldsay breed, the Shetland sheep have several primitive features (see Figure 5.3) such as a short tail, a tendency for the fleece to moult annually and for it to be coloured (Dun & Farnham, 2008). They are also a small, fine boned hardy species which has evolved in relative isolation in Shetland for around the last 1000 years (Butler, 2006). Like the North Ronaldsay breed, Shetland sheep were probably introduced to the Shetland Islands by Viking settlers (Dun & Farnham, 2008). They belong to the Northern European short-tailed group which also contains the Finnsheep, Norwegian Spaelsau, Icelandics, Romanovs and others. Classed as a primitive breed, the Shetland retains the hardiness, ease of parturition, longevity and ability to thrive on a low intake of feed common among such groups (http://www.shetland-sheep.co.uk/shetland.htm).

Figure 5.3: Shetland ewes and lamb (http://www.ansi.okstate.edu/breeds/sheep/shetland/Shet5.jpg and http://www.pembrokeshire-organic-holidays.co.uk/shetland_sheep.htm).

Figure 5.4: The wide range of fleece colours and marking in the Shetland sheep (http://www.kellas-stud.co.uk/shetland_sheep.htm).

Shetlands occur in some of the widest ranges of colours of any breed of sheep (see Figure 5.4). Besides white, the sheep produce several shades of wool including reddy / brown (moorit), silvery grey (shaela), fawn, grey, dark brown and black. They also have a wide variety of patterns and markings such as a white crown (krunet), dark belly (katmoget) and white or pale belly (gulmoget) (http://www.shetland-sheep.co.uk/shetland.htm). There are 11 main colours as well as 30 markings, many still bearing their Shetland dialect names. Unfortunately, many of these colours and markings have become quite rare as white wool has historically commanded a better price.

The population studied in this chapter comes from a single flock of Shetland sheep kept by Mary Jones and Roy Harris on South Walls, Hoy. Between 1992 and 1996 30 unimproved Shetland wethers and 12 unimproved Shetland rams from this population were slaughtered, with ages ranging from 7 to 52 months and 11 to 31 months respectively. The exact dates of birth and death are known for 18 of these wethers and for most of the remainder birth dates are known to within a week. Thirty four of these individuals that fulfilled all of the selection criteria outlined in chapter 4 were selected for inclusion in this study. As with the population from North

Ronaldsay, the majority of the animals from Hoy are born at the end of April, with a small number being born early in May. The population were kept on unimproved grass land with limited or no access to seaweed, and their diets were not supplemented. The terrestrial diet of these sheep is in direct contrast to those from North Ronaldsay, particularly with regard to their periods of nutritional stress. Unlike the animals from North Ronaldsay, the animals from Hoy will be in their peak condition over the late spring and summer months, when grass is abundant and the weather is clement.

5.2.3 Skara Brae

Skara Brae is one of Orkney's most iconic archaeological sites and one of Britain's most famous prehistoric settlements. It is located on Mainland in the western Parish of Sandwick in the bay of Skaill (see Figure 5.1 above). In the winter of 1850 a large storm combined with an exceptionally high tide stripped the grass from a large mound by the coast known locally as Skerrabra. It revealed the outline of a series of stone built houses (Childe & Clark, 1983). The local Laird, William Watt of Skaill began to excavate the site and by 1868 had uncovered the remains of four houses (Clark, 1976). In 1925 another storm damaged the site and during the construction of a seawall to protect the houses more structures were discovered.

Further excavations were carried out between 1928 and 1930 by Gordon Childe, uncovering a total of eight houses, linked together by a series of low covered passages (see Figure 5.6). There were almost certainly other houses in the settlement which have been eroded away by the sea. When the site was occupied the bay of Skaill would have been considerably smaller and the sea would not have been as close to the site as it is today. It is also possible that there was a fresh water lagoon located close to the site (Childe & Clark, 1983).

What makes Skara Brae so unusual and famous is the incredible preservation of the nucleated Neolithic village. Each house is built along the same style consisting of a large square room with a central fireplace. Opposite each fireplace is a shelved

dresser with bed on each side wall (See Figure 5.6). Radiocarbon dating carried out in the early 1970's disproved the earlier idea that the houses were Pictish and confirmed that the settlement was in fact Neolithic, dating between 3100BC and 2500BC. More recent radiocarbon dating carried out has suggested that the site was occupied between 4480 ^{14}C BP and 3930 ^{14}C BP (+/- 35 BP calibration not stated) (Pers. comm. David Clark). The settlement was built into or completely surround by midden deposits. These would have had the dual purpose of providing insulation and stability to the houses (Childe & Clark, 1983).

Figure 5.5: Showing the settlement at Skara Brae and the bay of Skaill (http://www.orkneyjar.com/history/skarabrae/).

The midden deposits surrounding the village contained large numbers of vertebrate remains, primarily cattle and caprine, indicating a heavy reliance on the products of these two species (Watson, 1931; Childe & Clark, 1983). Fishing also played a role in the economy of the village with limpets being used for bait and crab and shellfish being collected for food. Barley grains and hazelnut shells were recovered from the earlier layers of the midden (Rowley-Conwy in press). The sheep from Skara Brae are described by Watson (1931) as being almost as numerous as the cattle and as having 'remarkably long and slender limb bones'. Watson, (1931) also indicates that there was no evidence to suggest that the animals were killed off at the approach to

winter as was found in the cattle, suggesting that there was adequate natural biomass for the animals throughout the year.

Figure 5.6: Showing detail of the inside of one of the Skara Brae houses (Upex, 2009).

Due to the large size of the vertebrate assemblage and various time constraints on museum access and recording, a limited number of animal bone bearing contexts were targeted for analysis of caprine enamel hypoplasia. Contexts were selected that covered the oldest and the youngest periods of occupation at the site. The contexts were already securely dated through ^{14}C and a gap of around 300 – 400 years between the oldest and youngest occupation layers was revealed. The contexts studied and their dates are shown in Table 5.1.

Trench No	Context No	^{14}C Date (+/- 35 yrs calibration unstated)
1	102	3930 / 4030
1	162	4150 / 4245
1	157	4480
1	168	4480
1	154	N/A
2	213	4240 / 4245 / 4215

Table 5.1: The contexts studied from Skara Brae and their ^{14}C dates *

* These radiocarbon dates are reproduced here, prior to their publication, with the special permission of David Clark, Keeper of National Museums of Scotland, Archaeology Department and consequently are not to be reproduced without his permission.

5.3 Key research themes

Three broad and interlinking research themes are explored in this chapter:

Research Theme 1: Identifying general levels of population stress

This research theme fits into the second key research objective of this thesis – i.e. to understand the baseline causes of enamel hypoplasia and their implications for exploring animal management strategies. Using modern sheep data from Orkney, this theme is explored with regard to the identification of general stress levels within the populations, relating to their various known environmental and dietary factors involved in their growth and development. This then provides a baseline understanding of the impact of environment and diet on the formation and severity of enamel hypoplasias, which can then be used to investigate animal management strategies in an archaeological sample of Neolithic sheep from Skara Brae.

Research Theme 2: Seasonality

This theme deals with the identification and understanding of various seasonal factors such as diet, climate and physiology on the occurrence of enamel hypoplasia. This theme is investigated in two ways:

The seasonal occurrence of physiological events: All animals undergo similar periods of physiological stress such as weaning. This section investigates the use of enamel hypoplasia to identify these events within the modern and archaeological populations from Orkney.

The impact of seasonal dietary variation: The very different diets and seasonal period of under nutrition in the two modern populations provide the ideal opportunity to investigate whether differences in diet (and consequently different periods of nutritional stress) cause distinct variation in the frequency of enamel hypoplasia.

This will then allow the investigation and interpretation of enamel hypoplasia in archaeological populations with regard to seasonal dietary variation.

Research Theme 3: The interpretation of defect types and severity

Large modern data-sets present the ideal opportunity to investigate the possibility that different types and severity levels of enamel hypoplasia can be related to different forms and severity of stress event. This clearly links with the first major research aim of this thesis which is the development of a methodology for the recording and interpretation of enamel hypoplasia in caprines.

5.4 Results

A total of 85 mandibles from North Ronaldsay, 34 mandibles from Hoy and 90 isolated teeth from Skara Brae were recorded. The 85 mandibles from North Ronaldsay produced a total of 217 molars, of which 175 were complete and fully formed and 42 were still forming. The 34 individuals from the Hoy population produced a total of 95 molars, of these there were 30 complete and recordable first molars, 28 second molars and 18 third molars. Only 16 incomplete teeth from Hoy were recorded and of these only 1 showed evidence of hypoplasia. Of the 90 isolated teeth recorded in the Skara Brae material 28 teeth were recorded as having incomplete crowns, of these only 3 (11%) showed evidence of enamel hypoplasia. Only 4 (9%) teeth from North Ronaldsay that were still forming showed evidence of hypoplasia, with equally low numbers recorded in the developing teeth from the other populations (11% of incomplete crowns in both the Hoy and Skara brae datasets). Because of the low number of incomplete crowns showing evidence of enamel hypoplasia, it was decided to exclude developing teeth from the analysis due to the difficulties of relating teeth that have a root enamel junction (REJ) to those without an REJ. This will not affect the analysis of the distribution of hypoplasias on the tooth crown because, as discussed in Chapter 4, there are reduced numbers of enamel hypoplasias located in the upper part of the crown due to its rapid development. Of the remaining 175 complete teeth from North Ronaldsay, 147 were recordable, meaning that their enamel was not completely obstructed by dental calculus or cementum, which appeared to have formed extremely thickly in this population. A fact also noted by Britt and Baker (1990) which they suggest is due to the animals unusual seaweed diet.

5.4.1 Identifying general levels of population stress

Key points

There is a higher frequency of enamel hypoplasia (calculated using complete teeth) in the North Ronaldsay population than the Hoy population. This difference is highly significant ($\chi^2 = 0.0009$).

Skara Brae has a low frequency of enamel hypoplasia (calculated using complete teeth) compared to the two modern populations. This difference is also highly significant ($\chi^2 = 0.009$).

General results

The data discussed is shown in Table 5.2 below and a comparison of the relative frequencies between the three populations is shown in Figure 5.8. Of the final 147 complete teeth included in this study from North Ronaldsay 116 (79%) had hypoplasia present, amounting to a total of 241 hypoplastic events. These affected 94% of the total population studied. The defects affected 75% of all first molars, 83% of all second molars and 80% of all third molars. The average number of defects per molar was 1.4 defects for first molars, 1.7 defects for second molars and 2.0 defects on third molars.

Of the 34 individuals collected and studied from Hoy, 25 (74%) had hypoplasia. Sixty percent of all molars recorded from Hoy had enamel hypoplasia. Of the 18 individuals with all three molars present and complete 100% had enamel hypoplasia. For the individuals with only two molars present 70% had hypoplasia. Hypoplastic enamel defects in the Hoy population affected 48% of first molars, 75% of second molars and 72% of third molars. The average number of hypoplastic defects per molar was 0.4 for the first molars, 1.3 for the second molars and 1.4 for the third molars. There is a statistically highly significant difference ($\chi^2 = 0.0009$) between the two modern populations in terms of the frequency of enamel defects.

Out of the 62 complete tooth crowns studied from Skara Brae, 44% showed enamel hypoplasia. Contexts from the oldest and youngest periods of occupation at Skara Brae were investigated. Forty one complete teeth were recorded from the youngest context and just 21 were recorded from the older contexts. As there were no significant differences ($\chi^2 = 0.245$) noted between the upper and lower contexts in terms of hypoplasia frequency, the contexts will be discussed as a single assemblage. When this is compared to the two modern population there is a statistically significant difference in the frequency of enamel hypoplasia ($\chi^2 = 0.009$).

	North Ronaldsay	**Hoy**	**Skara Brae**
Total no. complete teeth	147	76	62
No. teeth with hypoplasia	116	46	27
% of complete teeth with hypoplasia	79 %	60 %	44 %
Number of individuals recorded	85	34	Cannot be calculated on isolated teeth
Number of individuals with hypoplasia	80	25	Cannot be calculated on isolated teeth
% of population with hypoplasia	94 %	74 %	Cannot be calculated on isolated teeth

Table 5.2: Comparing Orkney population in terms of frequency of enamel hypoplasia.

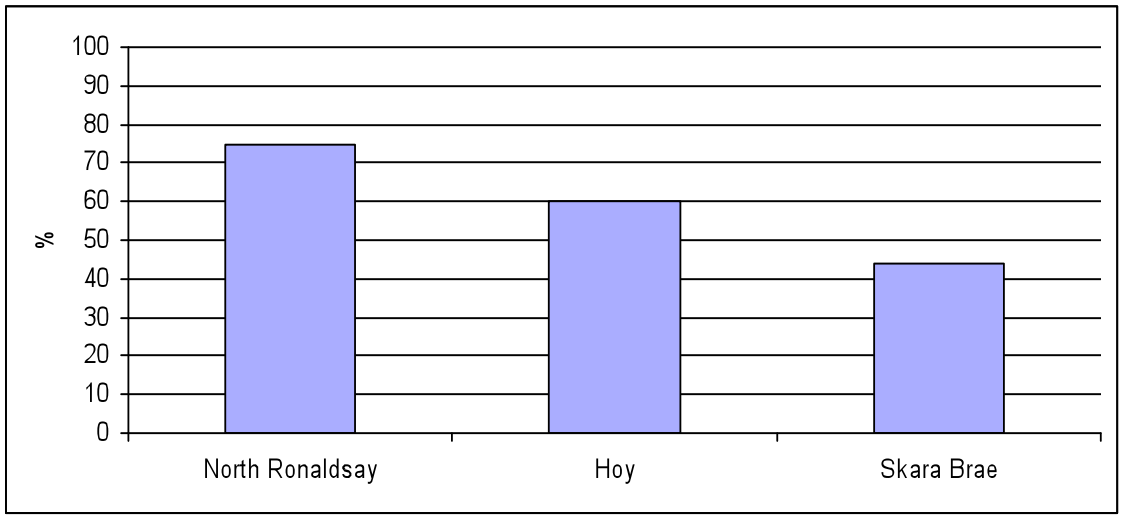

Figure 5.7: Comparing the percentages of complete teeth with enamel hypoplasia across the Orkney populations.

5.4.2 Seasonality

Key points

Enamel hypoplasia occurs in all three populations and on all three molars on the cervical half of the tooth crown.

In the North Ronaldsay population the numbers of defects peak when the animals are: 5/6 months old; 14/15 months old; and between 27 - 29 months old.

In the Hoy populations the numbers of defects peak when the animals are: 5/6 months old; 12 months old; and between 23 - 27 months old.

General results

The distributions of hypoplasia on the anterior and posterior cusps of the Orkney populations are shown in Figures 5.9 to 5.11. In the North Ronaldsay population, defects on the first molar are exclusively located in the cervical 21 millimetres of the tooth crown, with the majority of defects located in the 11 millimetres of the crown above the root enamel junction (REJ). A very similar pattern is seen on the second and third molars, with the majority of defects located in the cervical half of the tooth. On both the second and third molars there are very few defects located above 11 millimetres from the REJ.

The distribution of hypoplasia on the material from Hoy are very similar to the North Ronaldsay material in that the enamel defects are exclusively located in the cervical half of the tooth crown. In the North Ronaldsay dataset, on the second molar the maximum number of hypoplastic defect occurs between 2 and 3.9 millimetres above the REJ. In the Hoy data the maximum number of defects occurs higher up the crown between 6 and 7.9 millimetres above the REJ.

As with the material recorded from North Ronaldsay and Hoy, on the first and second molars from Skara Brae, almost all of the defects recorded occur in the bottom 20 millimetres of the tooth crown, with the majority occurring in the lowest

15 millimetres. On the third molar it is difficult to comment on the distribution of enamel defects due to the very small number of dental defects recorded - just five dental defects were recorded on the third molar. All of these defects occurred in the bottom 8 millimetres of the tooth crown (see Figure 5.11).

This data was then analysed using percentage running means. Unfortunately, the numbers of enamel hypoplasias recorded in the Skara Brae population were too small to be included in this analysis and the use of isolated teeth caused problems in the separation of the first and second molars. Results for the North Ronaldsay and Hoy populations are shown in Figures 5.12 and 5.13 plotted onto a schematic dental development graph (based on crown development models previously discussed in Chapter 4). An increase in the frequency enamel hypoplasias is observed on the first molar in the North Ronaldsay population around the time of birth, with a subsequent larger peak occurring at between 5 and 6 months after birth. On the second molar there is a steady increase in the occurrence of enamel hypoplasias, peaking at 14 to 15 months after birth and then dropping sharply. A similar picture is seen on the third molar, with the number of enamel hypoplasias increasing after 23 months and peaking at 27 to 29 months after birth.

In the material from Hoy the unusual distribution of enamel hypoplasia on the first molar is a result of the small dataset. However, there appears to be a peak occurring at around 5 to 6 months. On the second molar there is a wide distribution of enamel defects, peaking at 12 months after birth. The same is seen on the third molar, with the occurrence of enamel defects peaking around 23 to 27 months.

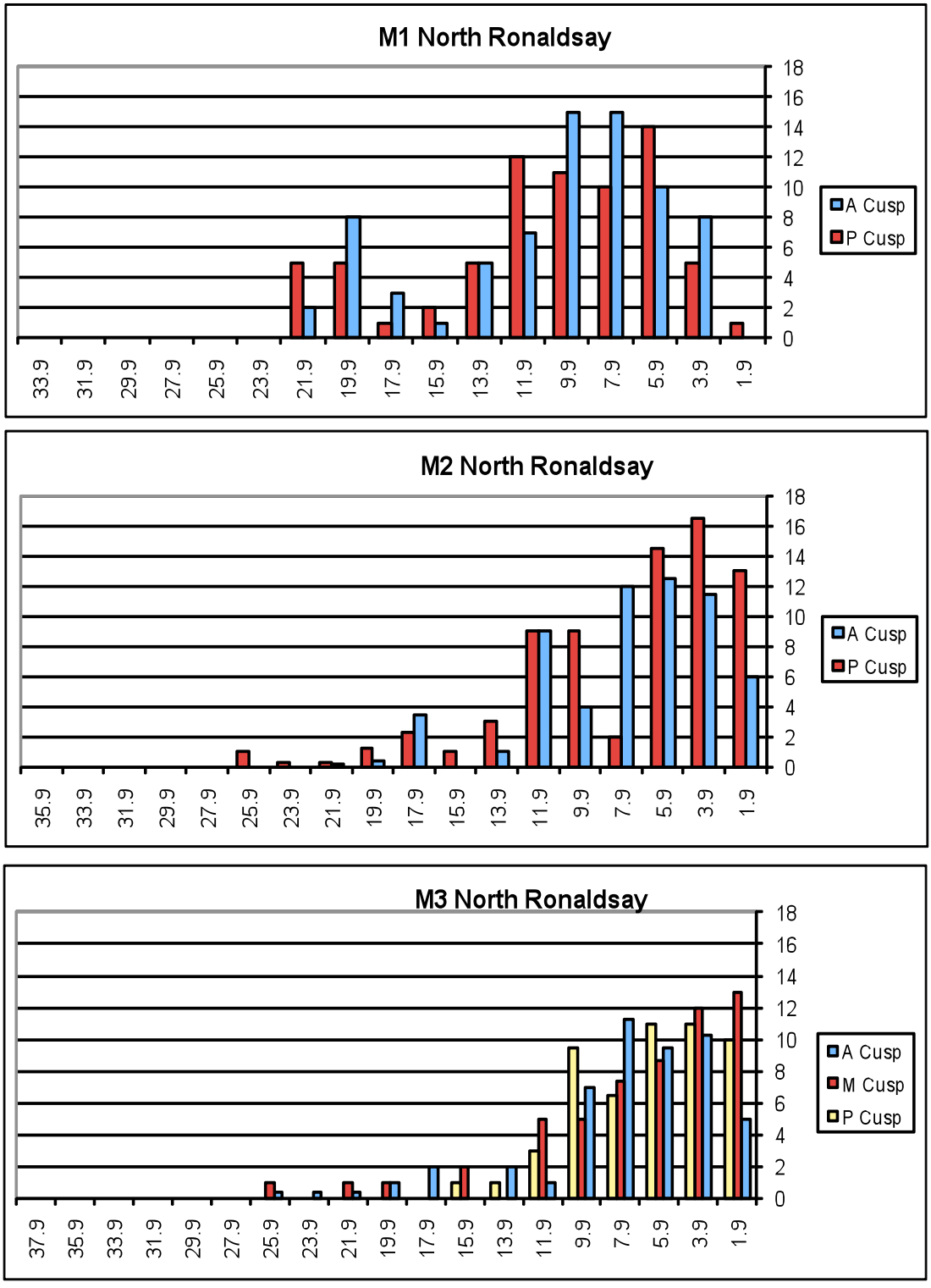

Figure 5.8: Distributions of enamel hypoplasia on molars from North Ronaldsay (2mm frequencies with the root-enamel junction at 0).

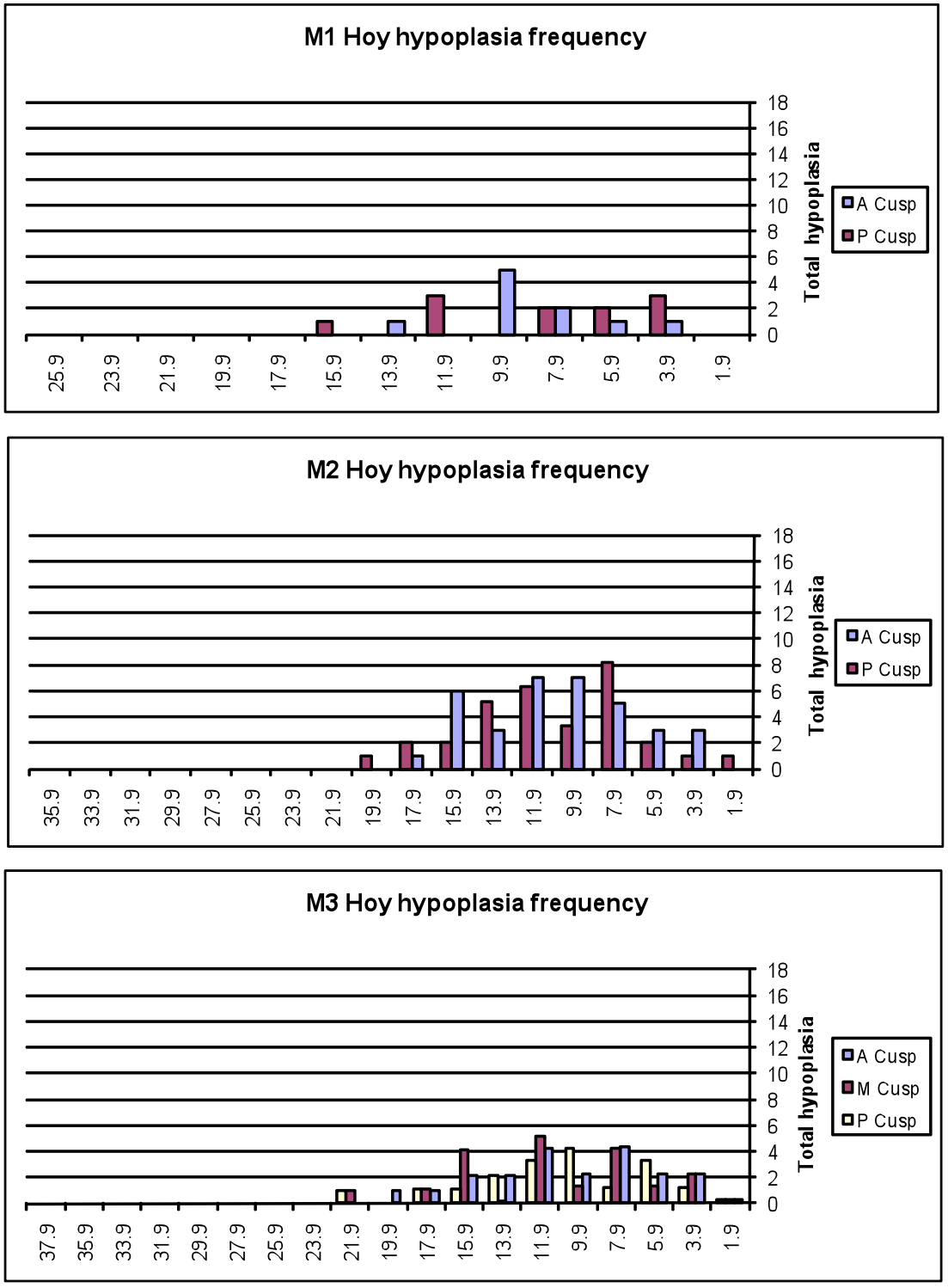

Figure 5.9: Distributions of enamel hypoplasia on molars from Hoy (2mm frequencies with the root-enamel junction at 0).

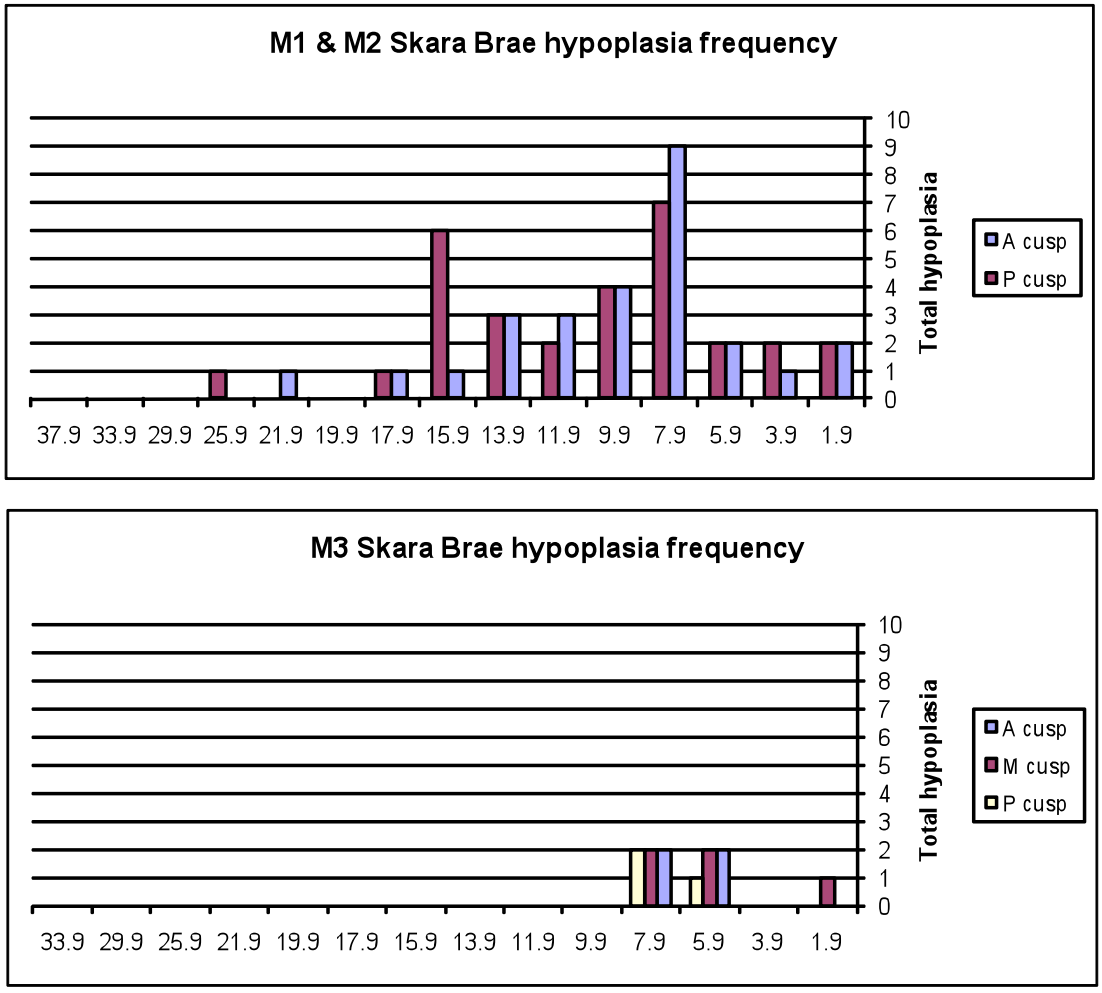

Figure 5.10: Distributions of enamel hypoplsia on molars from Skara Brae (2mm frequencies with the root-enamel junction at 0).

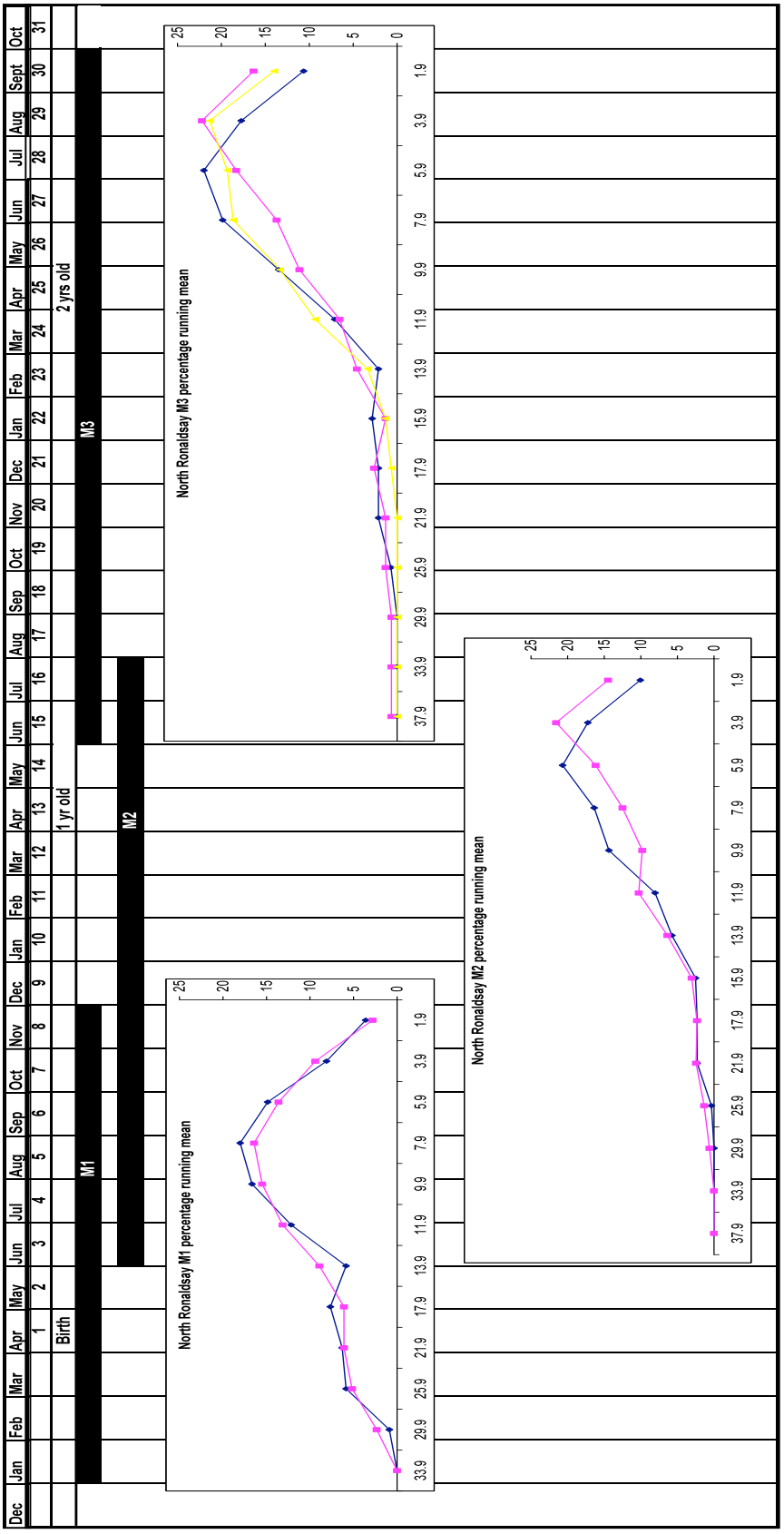

Figure 5.10: Showing the material from North Ronaldsay plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.

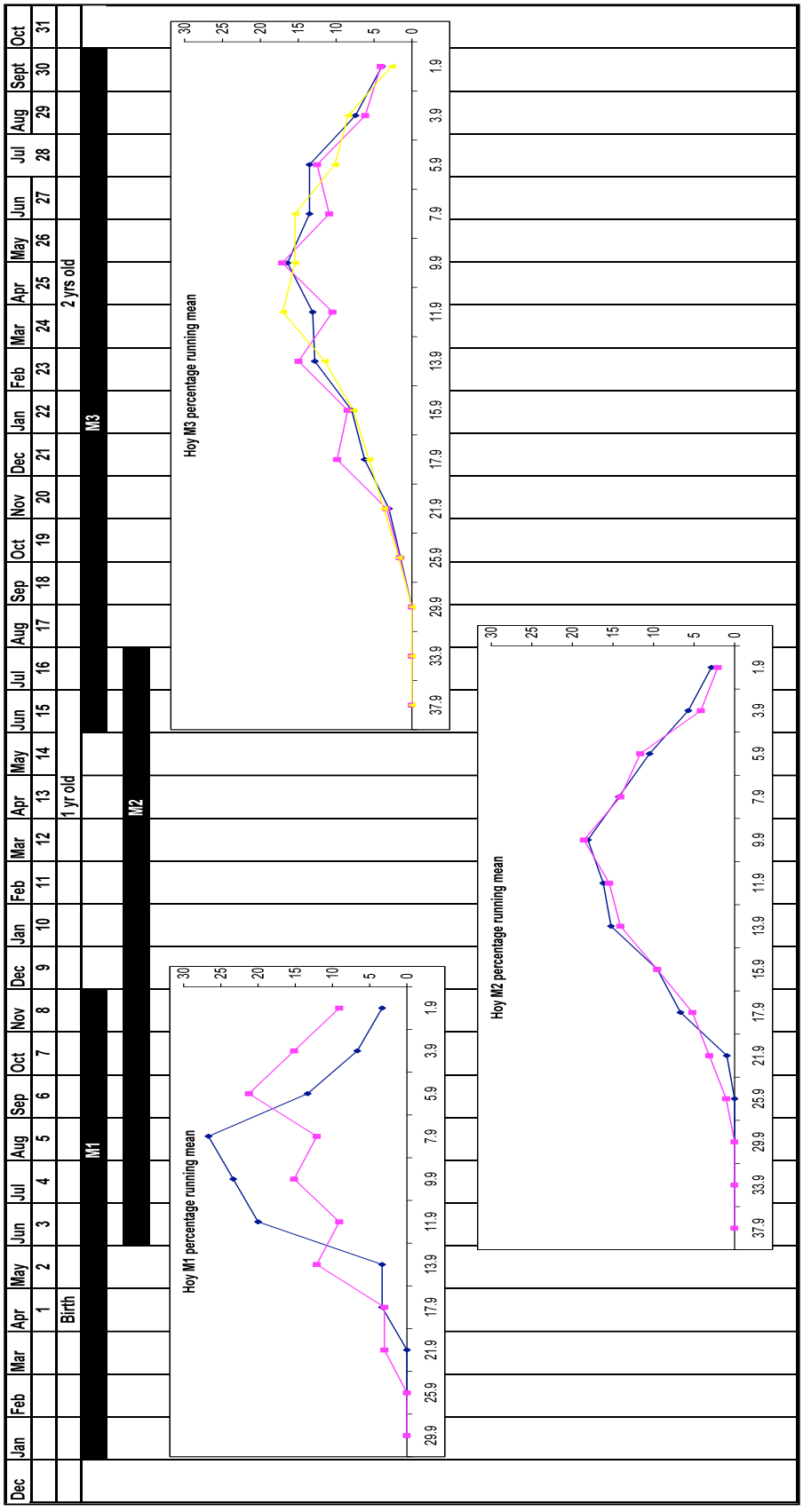

Figure 5.10: Showing the material from Hoy plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.

5.4.3 The interpretation of defect types and severity

Key points

The North Ronaldsay population has more severe defect types (such as lines) than the Hoy population, which has more low level extended defect types such as depressions.

The line-type defects from the North Ronaldsay population have a higher severity score (level 3 & 4) compared to line-type defects from Hoy.

The Skara Brae population has a high percentage of low level defects (depressions) compared to the modern populations.

Three key types of defect are identified in the North Ronaldsay population: lines, depressions and pits.

Differences occur in the chronological distribution of lines and depressions within the North Ronaldsay population

General results

The data discussed is shown in Table 5.3 & 5.4 and Figure 5.14 & 5.15 below. Within the North Ronaldsay population, line-type defects made up 67% of all defects recorded, 24% were depressions and 8% were pit defects. Of all the line-type defects recorded 77% were given a severity score of one, 14% were scored as two, 8% as severity level three and just 1% as level four. In the Hoy population, line-type defects accounted for 62% of all defects recorded, of the remaining defects 29% were depression defects and 9% were pit-type defects. Of all the line-type defects recorded, 88% were given a severity score of one, 8% were scored as two, 0% as severity level three and just 4% as a level four.

The very small number of enamel hypoplasias (42 in total) recorded from Skara Brae rendered many of the analyses statistically invalid. There were 14 (33%) line-type defects, 23 (55%) depression-type defects and 5 (12%) pit-type defects. The 14 line-type defects were recorded for severity producing 8 (57%) defects recorded as severity level one, 4 (29%) defects recorded at severity level two, 2 (14%) defects recorded at severity level three and no defects (0%) with a severity score of four.

	North Ronaldsay (n=242)	**Hoy (n=82)**	**Skara Brae (n=42)**
% of line-type defects	67 %	62 %	33 %
% of depression-type defects	24 %	29 %	55 %
% of pit-type defects	8 %	9 %	12 %

Table 5.3: Comparison of enamel hypoplasia types from all Orkney sites.

	North Ronaldsay (n=162)	**Hoy (n=50)**	**Skara Brae (n=14)**
% of line-type severity score 1	77 %	88 %	57 %
% of line-type severity score 2	14 %	8 %	29 %
% of line-type severity score 3	8 %	0 %	14 %
% of line-type severity score 4	1 %	4 %	0 %

Table 5.4: Comparison of enamel hypoplasia severities from all Orkney sites.

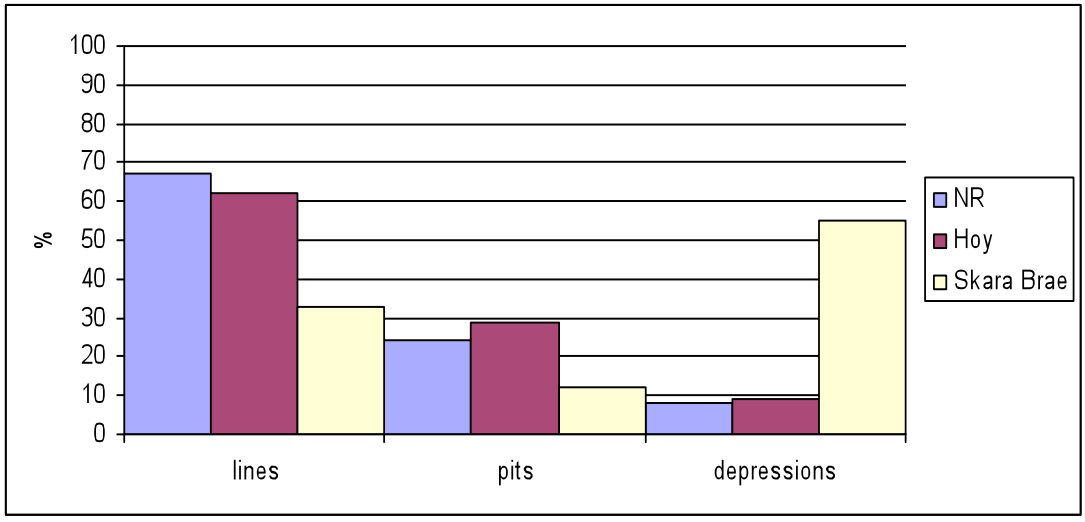

Figure 5.11: Comparing the percentage of different hypoplasia types between the Orkney populations.

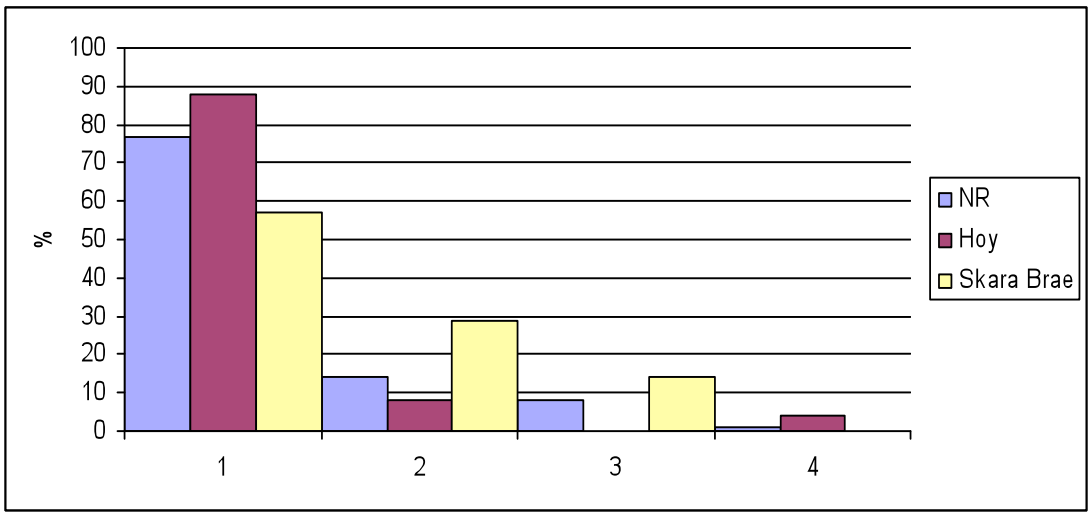

Figure 5.12: Comparing the percentage of different defect severity scores between the Orkney populations.

Within the North Ronaldsay population, there was also a possible fourth type of defect identified. This 'shift' type defect was identified in 15 of the North Ronaldsay first molars. Shift type defects are discussed in detail in section 5.5.3 and excluded from the following analysis for the reasons given there. The distributions of defect

types in the North Ronaldsay population are shown in Figure 5.16. A clear difference is seen in the distribution of line and depression-type defects. On the first molar a bimodal distribution of linear defects is seen, with defect peaks occurring at birth and at 6 months of age. Depression-type defects peak at 4/5 months after birth on the first molar. A similar distribution is seen on the second molar with linear defects peaking at 14/15 months after birth and depression-type defects peaking at 12 months after birth. Figure 5.17 shows the distribution of severity in linear defects from the North Ronaldsay population. This graph clearly shows that the majority of severe defects are located in the cervical half of the tooth.

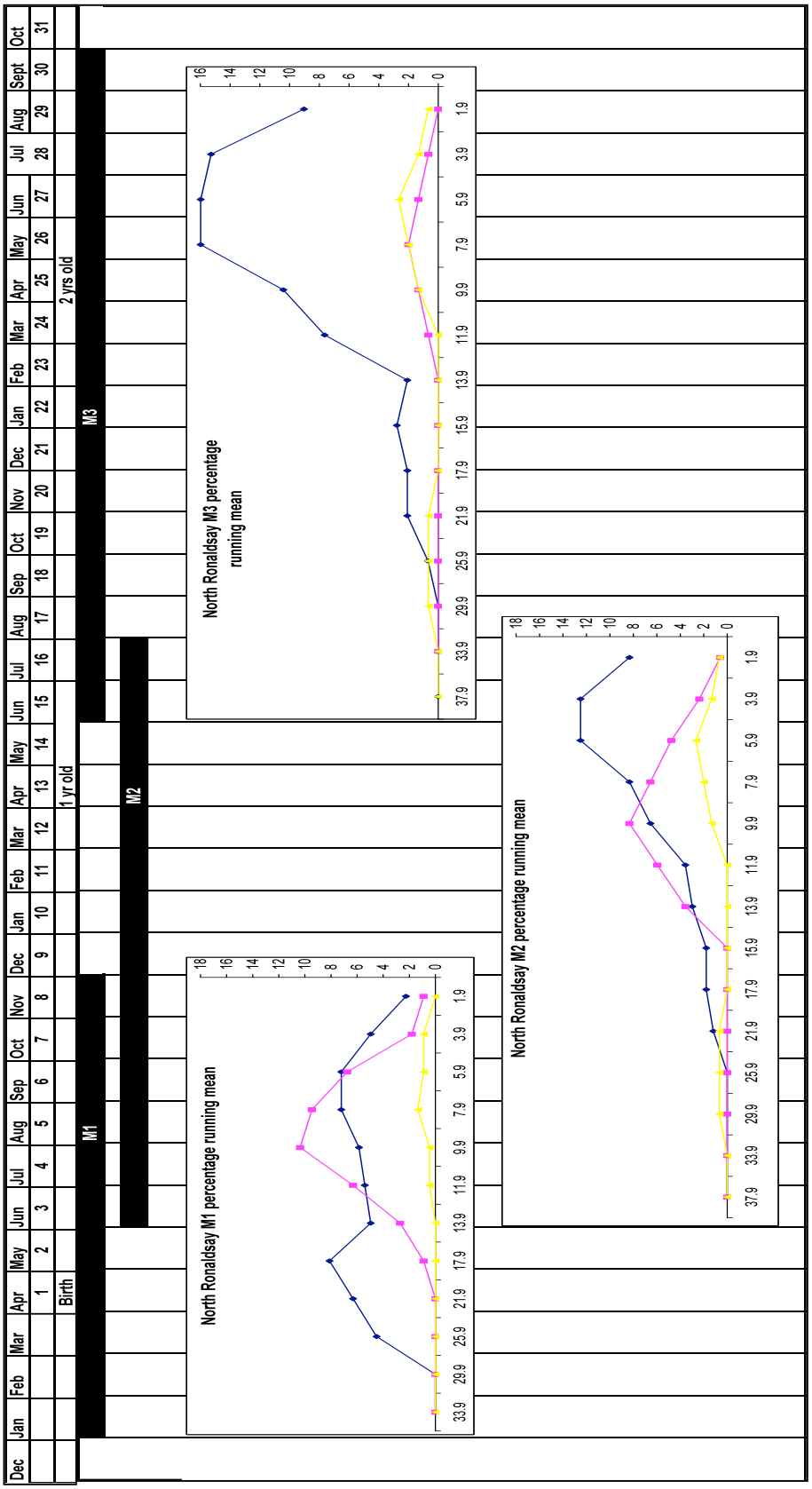

Figure 5.13: The material from North Ronaldsay plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present. Pink =depression defects , blue = line defects and yellow = pit defects.

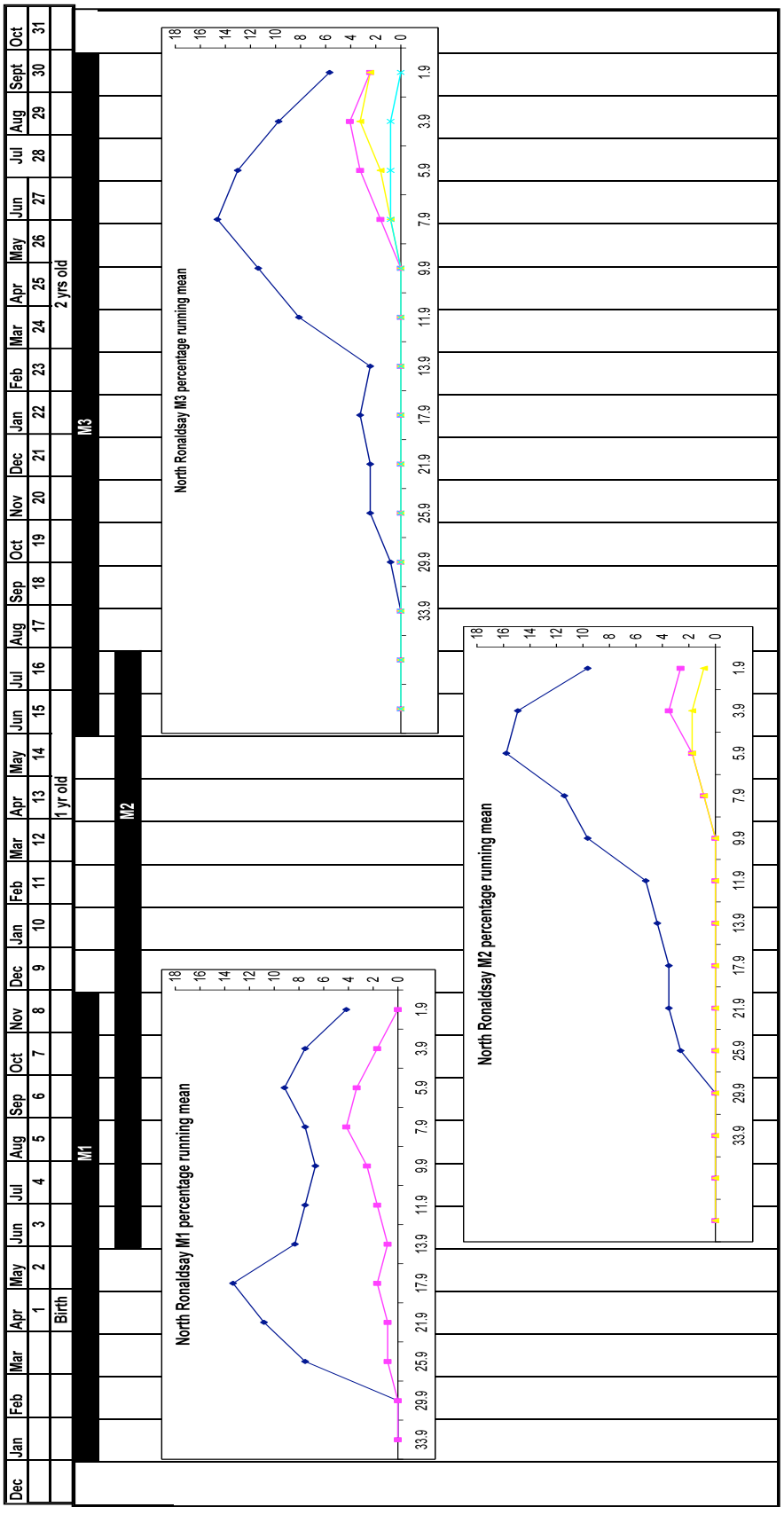

Figure 5.13: The material from North Ronaldsay plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.. Blue = Severity level 1, Pink = Severity level 2, yellow = severity level 3 and turquoise = severity level 4.

5.5 Discussion

5.5.1 Identifying general levels of population stress

As some individuals may not have had all teeth present or fully formed, the two modern populations were compared in terms of the total number of teeth observed with enamel hypoplasia. The harsher environmental and dietary conditions endured by the North Ronaldsay population appears to be reflected in the statistically significant, higher frequency of teeth affected by enamel hypoplasia.

Work by Britt & Baker (1990) supports the suggestion that the North Ronaldsay sheep have a more difficult and challenging lifestyle than previously assumed, leading to poor general health and malnutrition. In their 1990 study they carried out post mortem examinations of 71 North Ronaldsay sheep found dead on the island. Their research suggested that the animals may be less highly adapted to their unusual diet and difficult environmental conditions than previously inferred by authors such as Tribe and Tribe (1950), who suggested that the sheep 'are very healthy and suffer from few diseases'. In their study, Britt and Baker (opp. cit.) give the most common cause of death for young animals as malnutrition combined with heavy parasite loads. Older animals often die of starvation due to the excessive deposits of dental calculus causing dental disease leading to difficulty eating - a result of their unusual seaweed based diet. Other health problems were also identified by Britt & Baker (1990), including metabolic conditions such as the mineralization of the kidney and pneumonia.

The population from Hoy has a significantly lower frequency of enamel defects than the population from North Ronaldsay - interpreted here as a reflection of their less challenging environmental conditions and terrestrial diet - although they still show a relatively high frequency of enamel hypoplasia (60%). This may be related to their

lack of close management throughout the year when they are left to fend for themselves.

Interestingly, the ancient population from Skara Brae shows an extremely low percentage of enamel hypoplasia when compared to the two modern populations. This may suggest that the animals at Skara Brae may have suffered considerably less environmental and physiological stress than their modern counterparts from both Hoy and North Ronaldsay. There are two potential explanations for this reduced stress in Neolithic Skara Brae: 1) The animals were being managed differently at this site causing less physiological stress; 2) The seasonal variation in the availability of food was not so marked in the Neolithic due to better climatic conditions.

In both of the modern populations the animals are left to fend for themselves throughout the year, leading to seasonal periods of food shortages in their diets. The low frequency of enamel hypoplasia in the Skara Brae population may indicate that the animals were not run in an extensive agricultural system like the modern populations but were possibly kept on a small household scale and more carefully managed. For example, careful fodder management during the winter at Neolithic Skara Brae could have alleviated seasonal food shortages and reduced the number of enamel defects seen in this population. This is apparently supported by the preliminary analysis of the faunal assemblage by Watson (1931), where the age of the animals at death provides no clear evidence to suggest that there was a significant cull of individuals in the approach to winter, indicating that adequate natural fodder must have been available. It is of course possible that seaweed was used as a source of fodder for domestic livestock at Skara Brae, given the sites proximity to the sea and ongoing stable isotope work is further investigating this rather specialised aspect of possible ancient human husbandry (Balasse, pers. comm.).

Similar work already carried out at the Orcadian Neolithic settlement sites of Knap of Howar (dated to *c*. 3600 BC) and Holm of Papa Westray (dated to *c*.3000 BC) has

revealed lower levels of enamel defects in these archaeological populations (Balasse & Tresset, pers. comm.). At Knap of Howar, 50% of the complete mandibular teeth recorded had enamel hypoplasia, whilst at Holm of Papa Westray only 28% of all complete mandibular teeth recorded showed enamel hypoplasia (Balasse & Tresset, pers Comm.). An isotopic investigation of these two archaeological populations, revealed that at Knap of Howar, animals were grazing on terrestrial plants throughout the year, but at Holm of Papa Westray, the isotopic evidence suggested a significant seaweed contribution to the diet (Balasse, et al. 2006). The highest carbon isotope values in the Holm of Papa Westray individuals sampled occurred during the winter months, inferring that the animals were eating fresh seaweed, rather than dried seaweed, and thus were probably herded onto the beach as seen in the North Ronaldsay population (Balasse, et al. 2006). It may be that the low levels of enamel hypoplasia seen in the sheep population from Holm of Papa Westray reflect a year-round supply of fodder (both in grass and seaweed form), and that the higher levels of enamel hypoplasia seen at Knap of Howar are related to seasonal food shortage as seen in the two modern populations. This would support the suggestion that the low frequency of enamel hypoplasia in sheep revealed in the Skara Brae sample, relates directly to a husbandry strategy that alleviates seasonal food shortages through the provision of seaweed fodder.

The fact that all three of these archaeological populations show lower general frequencies of enamel hypoplasia than their modern counterparts supports the possible interpretation of small scale, carefully managed husbandry systems operating in the Neolithic of Orkney. Alternatively the climatic variation and change in the flora and soils of the island between the Neolithic period and modern times may also be responsible. Davidson, et al. (1976) and Bunting (1994) both suggest that the modern climatic features of the Orcadian landscape are little changed since the Neolithic. However, researchers have long argued that during the Bronze Age, the climate became increasingly cool and damp (Frenzel, 1966; Pennington, 1969; Burgess, 1985; Wittington & Edwards, 2003). Frenzel (1966) suggests that this began in *c*.35000 B.P and that it had intensified by *c*.29000 BP. It is suggested by

Keatinge & Dickson (1979) that this increasingly cool damp climate may have contributed to the development of blanket peat over parts of the Orcadian landscape. Their analysis of pollen cores from four locations in Orkney revealed that during the Neolithic period, the tall herb and fern plants from the shrub understory gave way to extensive open pasture - a likely result of grazing pressure (Keatinge & Dickson opp.cit). They also conclude that the extensive open pasture land has subsequently changed little since the Neolithic period, with the exception of certain areas where blanket peat has formed. They suggest that blanket peat formation began c.34000 BP due to a combination of climatic deterioration and human impact on the landscape (Keatinge & Dickson, 1979). Bunting (1994; 1996) also agrees that there is vegetative change within Orkney, including the development of blanket peat, but suggests that climate change is just one of a myriad of potential factors, including human impact, soil leaching and podsolization. Bunting (1996) clearly demonstrates this increase in blanket peat bogs in pollen samples from the Loch of Knitchen, where at the beginning of the Neolith period there was less than 10% of pollen from bog loving plants such as *Calluna vulgaris* compared to 45% in more recent times.

Given that the evidence suggests a slightly milder, dryer climate during the Neolithic and a higher availability of grazing land (as the peat bogs had only just begun forming) the biomass availability was greater during this period than the present day. Reduced levels in available biomass obviously will lead to increased seasonal grazing pressures and reduced winter foddering, and – it is postulated – higher frequencies of enamel hypoplasias. Conversely, the higher level of available biomass in the Orcadian Neolithic may serve as an explanation for the observed lower numbers of enamel hypoplasias in the Neolithic populations.

5.5.2 Seasonality

In Orkney, unimproved sheep breeds give birth within a tightly defined season between April and May, with the majority of individuals being born between the 3rd week in April and the 1st week in May (Morris, 1999). This allows the data to be confidently plotted against a known calendar of seasonal events, as the tightly defined birthing season causes seasonal factors (e.g. temperature and food availability) to impact on all individuals within the same period of dental development. When the enamel hypoplasia distributions are adjusted for different rates of tooth crown development, and then plotted using running means (as discussed in Chapter 4), very clear peaks in the occurrence of hypoplastic defects become visible which can be related to specific seasonal events affecting these populations. Unfortunately the number of enamel hypoplasias recorded from Neolithic Skara Brae was too small to make this kind of analysis statistically meaningful. As a result, these data are excluded from analysis.

<u>The seasonal occurrence of physiological events</u>

As discussed previously in Chapter 4, crown formation of the first molar begins *in utero* and finishes at approximately 8 months after birth. Two apparent peaks of enamel hypoplasia occur on the first molar in the North Ronaldsay population in this time period (see Figure 5.12 above). The first (and smallest) peak of enamel hypoplasia coincides with birth, which occurs in late April and the 1st week of May in the Orkney sheep populations. Birth produces multiple forms of stress, including temporary malnutrition and rapid environmental change, and this is most likely the cause of this early peak of enamel hypoplasias in Orkney sheep. A similar conclusion – i.e. physiological stress caused during and immediately following birth - has been drawn by Dobney & Ervynck (2000), who identified an identical early peak of enamel hypoplasias in the first molars of archaeological pigs. The development of enamel hypoplasia in relation to stress caused by birth has also been noted in humans, with the identification of the so called 'neonatal ring' identified by Sarnat and Shour (1942).

The second peak of enamel hypoplasia observed on the first molars of the North Ronaldsay population, appears to occur approximately five months after birth, and correlates with the return of the females with their young to the beach (see Figure 5.12 above). Weaning of the lambs would have also been occurring during this period, and although it is allowed to occur naturally in the North Ronaldsay population, it can still be considered a nutritionally stressful period for young animals as they are slowly forced to adapt to a radically new diet. The move from terrestrial to beach grazing likely exacerbated any nutritional stress caused by weaning, and produced a variety of physiological stress events, linked with the radical dietary shift from grass to seaweed.

The animals from Hoy have an identical season of birth to those from North Ronaldsay, which is unsurprising given their close geographic proximity to one another. As previously discussed, the date of birth of all the animals from Hoy is known to within one week. Consequently the enamel hypoplasia can be confidently plotted onto the same developmental calendar as the animals from North Ronaldsay (shown in Figure 5.13 above). A very similar distribution of enamel hypoplasias on the first molar can be seen in both the Hoy and North Ronaldsay samples. However, there are subtle differences. The first molar in the Hoy population shows one large peak of enamel hypoplasia located in the centre of the occlusal half of the crown, between five and six months after birth. This is can be confidently correlated with the occurrence of weaning in this population. As with the North Ronaldsay population, weaning was allowed to occur naturally in the Hoy animals and consequently is a slow process occurring over several months. However, in normal populations complete separation between the lamb and its mother has occurred by 8 months (Squire, 1975). This fits with the occurrence of enamel hypoplasia peaks at around 6 months, as the animal is adjusting to a new diet. The lack of a peak indicating birth in the Hoy population may suggest that birth is a less stressful event compared to the North Ronaldsay population. However, the number of enamel

hypoplasias located on the first molar in this population is considerably smaller than that of North Ronaldsay, demonstrated by the fact that even though the data is shown as running means it still does not produce a smooth curve. The small number of enamel hypoplasias on the first molar may therefore potentially obscure any peak related to birth.

The impact of seasonal dietary variation

Figures showing the distribution of enamel hypoplasia for the Hoy and North Ronaldsay populations are shown in Figure 5.18 and Figure 5.19 plotted against a calendar of seasonal events. In the North Ronaldsay population there is only one clearly defined peak of hypoplasia on the second molar in the lower half of the crown occurring between 12 and 15 months after birth (March – June). While there are no obvious physiological stress events occurring during this period of the animals' lives, there are various seasonal events which could explain the presence of this peak. All of the animals are born in a tightly defined 'season of birth' between April and May. Consequently, as the North Ronaldsay animals are completing the growth of the second molar, they are entering into a period of nutritional stress, caused by the onset of the summer months and a reduction in the amount of seaweed available. This is a particularly challenging period for the North Ronaldsay population, as the winter storms abate, the quantity of seaweed washed up on the beach decreases, leading to weight loss, and under-nutrition (Morris, 1999; Gourley, 2006). According to Brit and Baker, (1990) starvation and malnutrition accounts for 24% of all deaths in the North Ronaldsay population.

The brown *Laminaran* seaweeds which are the principle dietary component for the North Ronaldsay sheep also renew their fronds in the spring months, casting off their old fronds prior to the growth of new ones. This means that there is more food available during early spring than there is later in the year (Hall, 1975). Mann (1973) demonstrated that the chemical composition of seaweed alters throughout the year in relation to seasonal growth patterns. The variable chemical and consequently

nutritional level of seaweed combined with studies by McNaugh, et al. (1954) into the digestion process of North Ronaldsay sheep, led Hall (1975) to conclude that, while there are large quantities of seaweed available in early spring, it is at this time when its nutritional content may be the lowest. This is supported in a study by Britt & Baker (1990), who suggest that *Laminaran* washed ashore in May has high water content and may provide insufficient calories. They also state that the condition of the animals was generally worse in the spring and that in October, by comparison, the animals were 'quite fat and showed new wool' growth (Britt & Baker, 1990: 131). However, Brit and Baker also indicate that in mid-summer the condition of the animals varied according to their location on the island and that those from the north were in extremely poor condition.

The third molar begins forming in approximately the fifteenth month of life and is completed at approximately thirty months (see Figure 5.18). The distribution of the enamel hypoplasias again shows a clear peak in the lower half of the crown between 24 and 29 months (March – August). Again this coincides with the summer months and the period of nutritional stress caused by a lack of available seaweed. For females in this population there is potentially the additional stress of their first pregnancy during this period. This would produce a series of associated physiological stresses, including being moved inland and onto a copper-rich terrestrial diet. The large number of impacting factors may be responsible for the slightly broader chronological distribution of enamel defects on the third molar. Alternatively, the longer and more variable period of dental development occurring in this tooth may also be a factor.

Clearly there is some disparity between sources about the exact period of maximum nutritional stress in the North Ronaldsay sheep population. However, all of the sources available indicate that the spring months produce seaweed with low levels of nutrition and the summer months lead to a reduction in the amount of seaweed fodder available. The papers discussed above, combined with observations from

locals stating that the animals gain weight in the winter months, and the fact that the mutton market for North Ronaldsay sheep is closed in April due to the poor quality of the animals, all combine to suggest that the spring and summer months are a nutritionally difficult time for the North Ronaldsay sheep, with the animals gaining weight and condition from the end of summer onwards as the winter storms being to wash large quantities of nutritional rich seaweed onto the shore. This summer period of poor nutrition clearly correlates with the increase in the frequency of enamel hypoplasias affecting the second molar between March and July and the third molar between March and August.

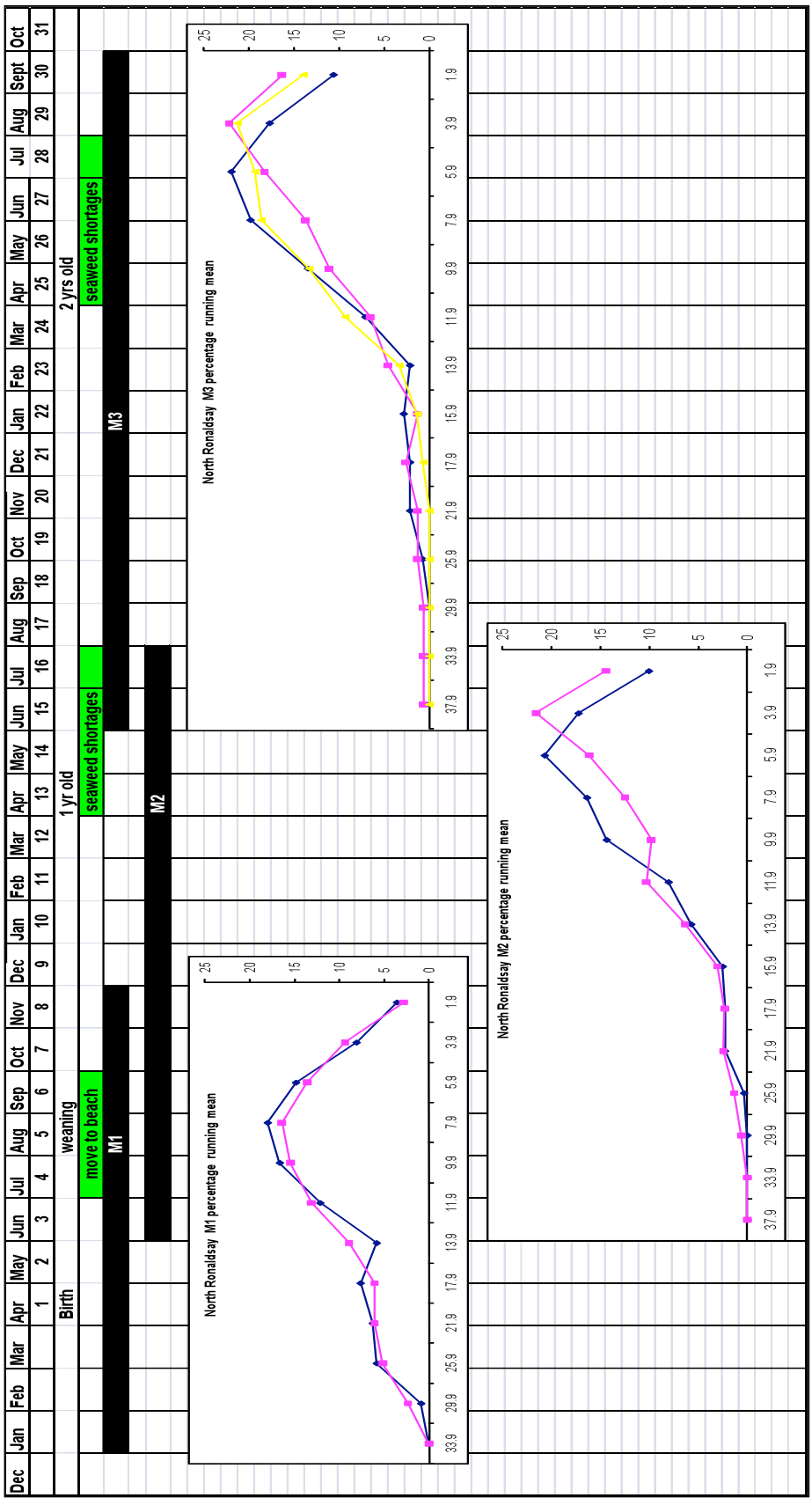

Figure 5.13: The material from North Ronaldsay plotted as percentage running means onto a chart of tooth development rates. Months after birth and physiological and dietary stressors are marked along the top of the figure. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of enamel hypoplasia present.

The Hoy dataset, just as in the North Ronaldsay samples, shows a single peak of enamel hypoplasia on the second molar, but it occurs several months earlier than the peak in the North Ronaldsay population (See Figure 5.19). It's relative position on the tooth crown correlates with tooth development occurring during spring (January to March), a period which is traditionally very difficult for domestic animals in terms of food availability (Mainland, 2000). It is this time of year, just before the grass begins to grow again, when winter fodder supplies are often exhausted, leading to food shortages and malnutrition. February is also on average the coldest month of the year, with mean temperatures of 3^{o}C, potentially also contributing to additional physiological stress suffered in this period.

A very similar peak of enamel hypoplasia was also observed on the third molar, correlating with crown development stages occurring between February and June (See Figure 5.19). This peak is again assumed to be related to early spring fodder shortages. As seen in the North Ronaldsay population, the peaks of enamel hypoplasia occurring in the third molar occur over a longer developmental period and do not appear to match up so closely with the hypothesized periods of nutritional / environmental stress as the peaks of hypoplasia seen in the second molars. This is almost certainly due to the longer and more varied period of development in the third molars, leading to greater variation in the enamel development rates occurring down the tooth crown.

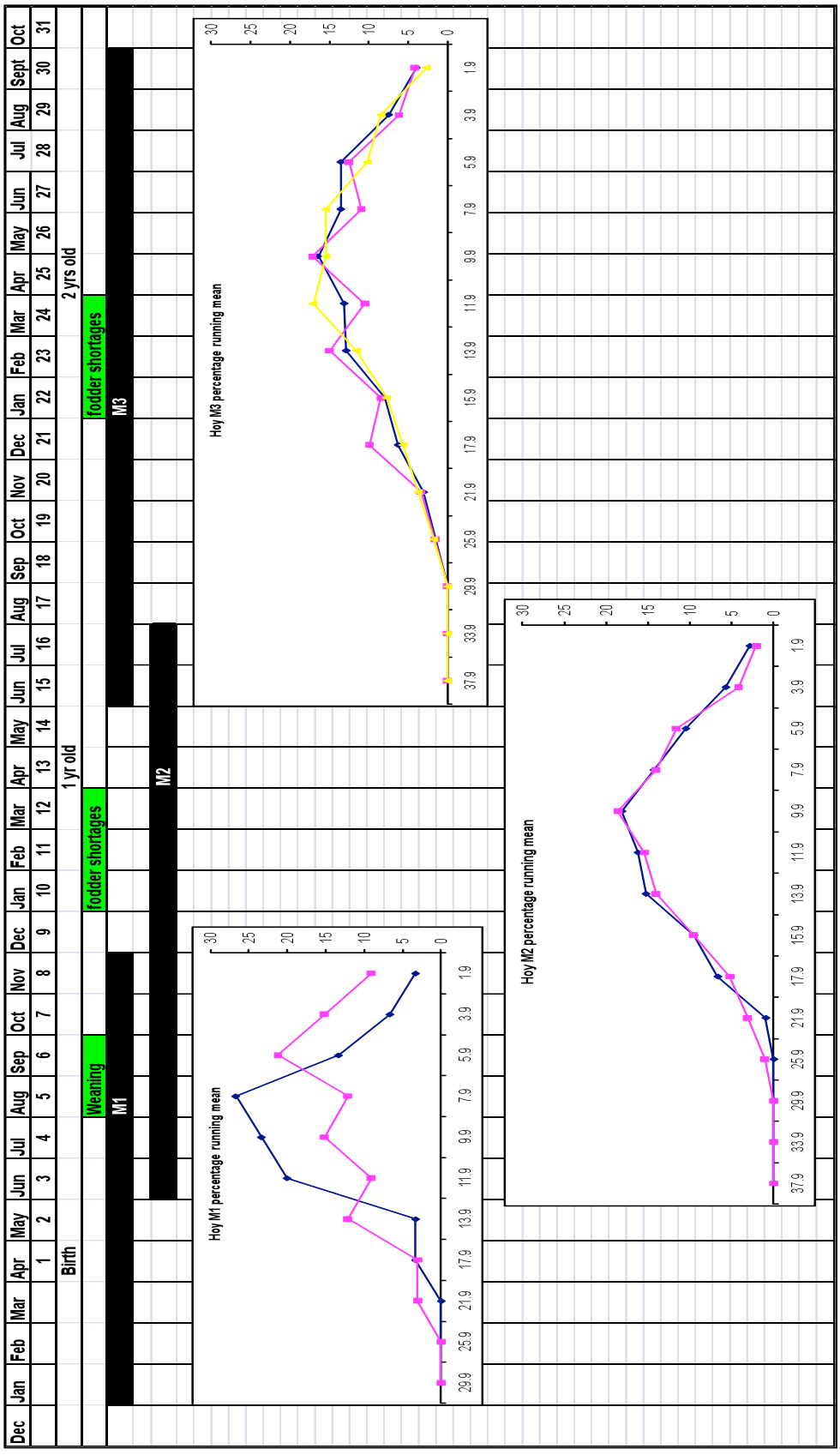

Figure 5.13: The material from Hoy plotted as percentage running means onto a chart of tooth development rates. Months after birth and physiological and dietary stressors are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.

5.5.3 The interpretation of defect types and severity

Work by Witzel, et al. (2006) demonstrated that different forms of enamel hypoplasia could be related to different types of stress event occurring in the lives of pigs. It was demonstrated that depression-type events were indicative of long lasting but low intensity periods of stress, whereas linear and plane-type defects (probably recorded as severe lines) are caused by a severe stress impact with a shorter time duration (Witzel, et al. 2006). Further work (Witzel, et al. 2008) undertook a more detailed histological investigation into the different types of defects and their formation processes, and demonstrated that different intensities and durations of stress events can produce different forms of defect, dependant on the secretory stage of the ameloblasts affected. This is discussed in more detail in Chapter 3.

Comparing populations

The suggestion that an increased frequency of enamel hypoplasia is a reflection of the harsher environmental and dietary conditions faced by the North Ronaldsay population, is also further supported by the types and severity levels of the hypoplastic enamel defects recorded. The North Ronaldsay population reveals a higher frequency of severe defect types (such as lines) when compared to the Hoy population, which has more low-level defect types such as depressions. The line-type defects from the North Ronaldsay population also have higher overall severity scores (level 3 & 4) compared to line-type defects from Hoy (see Table 5.4 in section 5.4.3 above). Defect analysis from the Skara Brae population also supports the suggestion that defect types and severity reflect population stress. The Skara Brae population has a very low frequency of enamel hypoplasia, interpreted as lower levels of environmental and dietary stress than the two modern populations. This is supported by the high frequency of depression-type defects seen in this population (see Table 5.4 in section 5.4.3 above).

Defect type

This section of the analysis deals only with the population from North Ronaldsay. This population provided the largest dataset recorded in this study, both in terms of the number of teeth available for study and the number of hypoplasias produced. For ease of analysis and graphic representation, only the distributions on the anterior cusps are plotted, but this does not affect the data in any way for, as demonstrated above in Figure 5.9, the distribution of defects on the anterior and posterior cusps is almost identical.

The distribution of lines, pits and depressions is shown plotted against a seasonal calendar to attempt to investigate if there is any link between different types of defect and different seasonal events. Identical adjustments are made, taking into account the variation of growth down the tooth crown and the distributions are shown as relative frequencies of the total number of enamel hypoplasias found on each molar. Figure 5.20 shows the distribution of the types of defects recorded in relation to the seasonal and physiological events occurring during the period of tooth development in the North Ronaldsay population. As linear type defects are the most common form of hypoplastic defect in the North Ronaldsay population, it is no surprise that these dental defects clearly map onto the peaks of hypoplasia relating to the physiological and seasonal events discussed above. Pits are a relatively rare form of enamel defect and consequently any interpretations about their links to different types of seasonal events is very difficult, although they do appear to peak in similar locations to the linear type defects. Of greatest interest to this discussion are the depression-type defects which, on the first and second molars, follow a different distribution pattern from the linear defects.

On the first molar, linear type defects are the only type identified relating to birth, supporting the assumption that birth causes a short period of physiological stress relating to both the physical trauma as well as the short period of malnutrition immediately following birth as the animals adapt to a new diet and environment. The

frequency of linear defects then remains moderately high in the months immediately following birth, before reaching a small peak in September. This is the time of year when the North Ronaldsay females and their young are returned to the beach. Again this small peak is probably related to a change in diet and environment as the animals adapt from the relative safety of the inland terrestrial grasses to life on the beach eating seaweed. The depression-type defects follow a different pattern. There appears to be just one peak of depression-type defects on the first molar, occurring between July and August. A similar separation between the line and depression-type defects is also seen on the second molar, where linear type defects peak between May and June and depression-type defects peak in March.

There are several possible explanations for the differences between linear and depression-type defects in the North Ronaldsay population. As discussed above, work by Witzel, et al. (2006; 2008) demonstrated that depression-type defects in low crowned species such as pigs and humans can be related to long duration minor impact stress events such as malnutrition during the winter months. If this is also the case in high crowned species then it could be suggested that weaning is responsible for the peak in depressions on the first molar, by causing an extended period of low level stress as the animal adapts to a solid diet and increasing separation from the mother. On the second molar, the peak in depression-type defects in spring could be explained by a period of minor malnutrition relating to the low nutrient values found in seaweed during this period. Alternatively, it could be a reflection of the often severe weather experienced in Orkney during February. However, if this was the cause of the depression-type defects, then a similar pattern would be expected in the third molar, with a peak in depression defects occurring in March, but this is not the case. On the third molar depression-type defects account for just 6% of all defects on the anterior cusp compared to 32% on the first molar and 39% on the second molar.

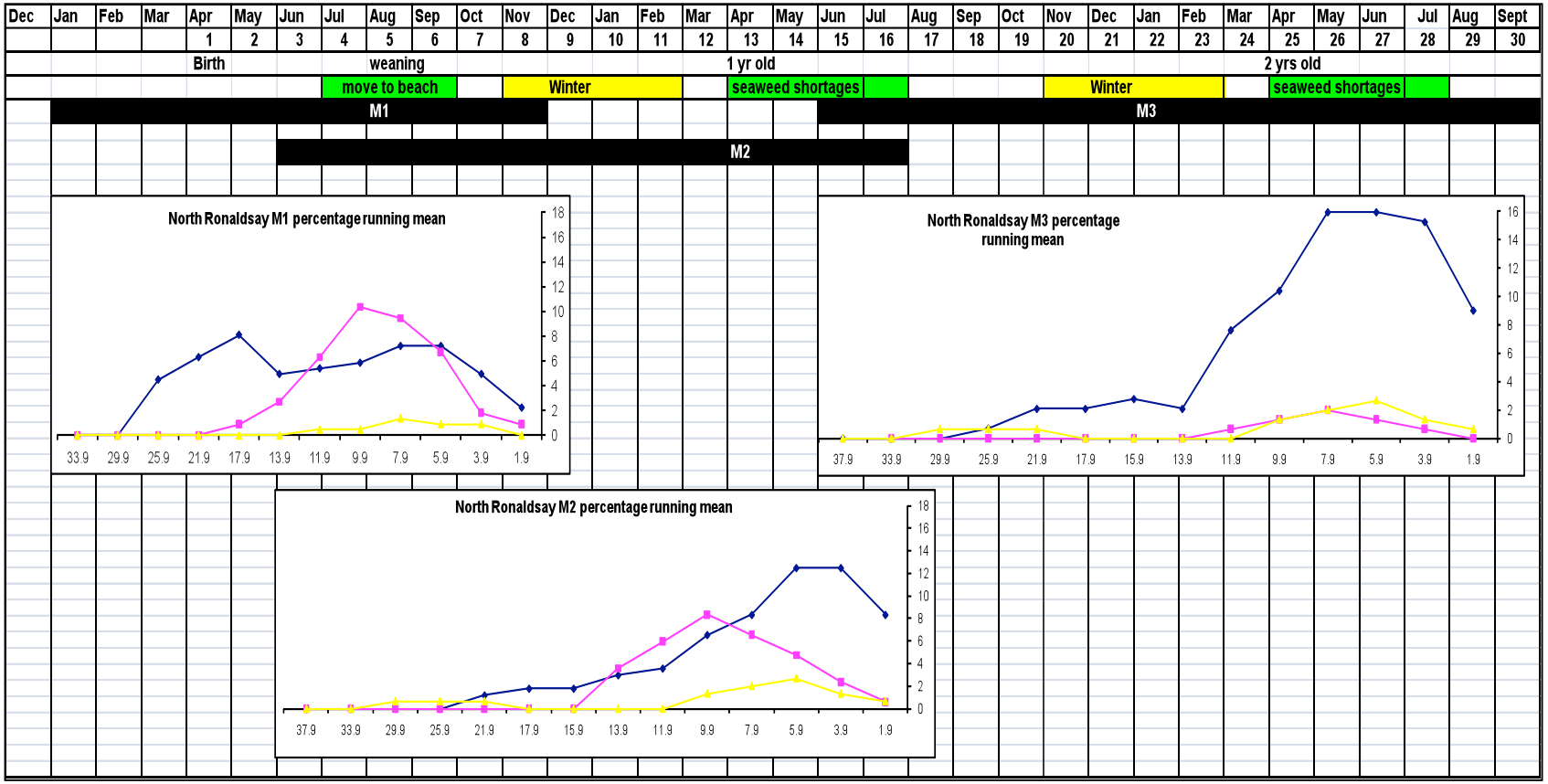

Figure 5.13: Showing the defect types from North Ronaldsay plotted as percentage running means onto a chart of tooth development rates. Months after birth and physiological and dietary stressors are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.. Pink lines =depressions, blue lines = lines and yellow =pits.

Very early on in the recording of the North Ronaldsay population, an unusual feature of the crown occurring in the first molars was identified. It was described and recorded originally as a 'shift type' dental defect, whereby the cervical half of the crown 'doglegs' in a posterior direction (see Figure 5.14).

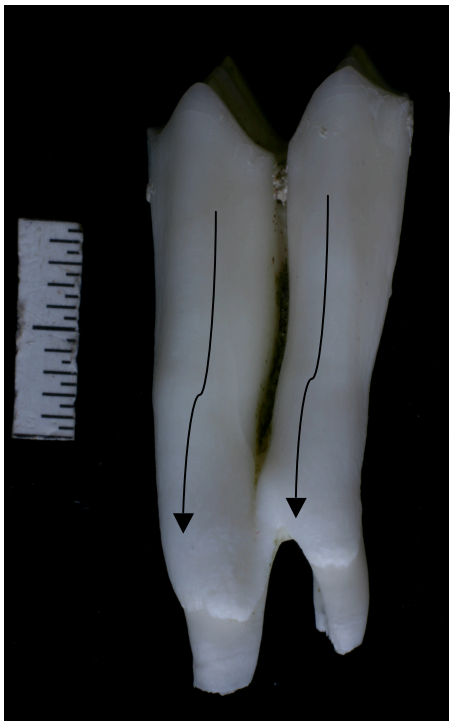

Figure 5.14: Shift in trajectory of crown direction- North Ronaldsay sheep first molar.

However, further research and histological analysis has indicated that this crown formation is not a pathological dental defect, but is most probably caused by the development, eruption and shedding of the surrounding teeth. It is suggested that as the deciduous and other teeth grow, erupt and are shed, they exert various pressures on the developing tooth crown that they surround, causing the developing crown to alter accordingly. These crown variations or 'shifts' have been noted in several of the populations studied in this research but appear to be most prevalent in the North Ronaldsay and Kenyan populations. It may be that these very small, unimproved species have restricted space in their mandibles, causing greater pressures to be

exerted on the developing teeth, similar to the problems faced by many humans with the eruption of their third molars. While these defects most commonly cause an anterior to posterior shift in the crown they can also cause a lingual – buccal shift, which appears identical to a depression-type hypoplastic defect (this can also be seen in Figure 5.14 above).When the occurrence of these 'shift type' defects on the first molar is plotted in relation to the occurrence of depression-type defects as shown in Figure 5.22 there is striking similarity in the frequency distribution of these defect types. This may suggest that depression-type hypoplastic defects recorded in mid-crown locations in high-crowned species are related not to physiological or nutritional stress but rather to the simple development and growth of the tooth crown.

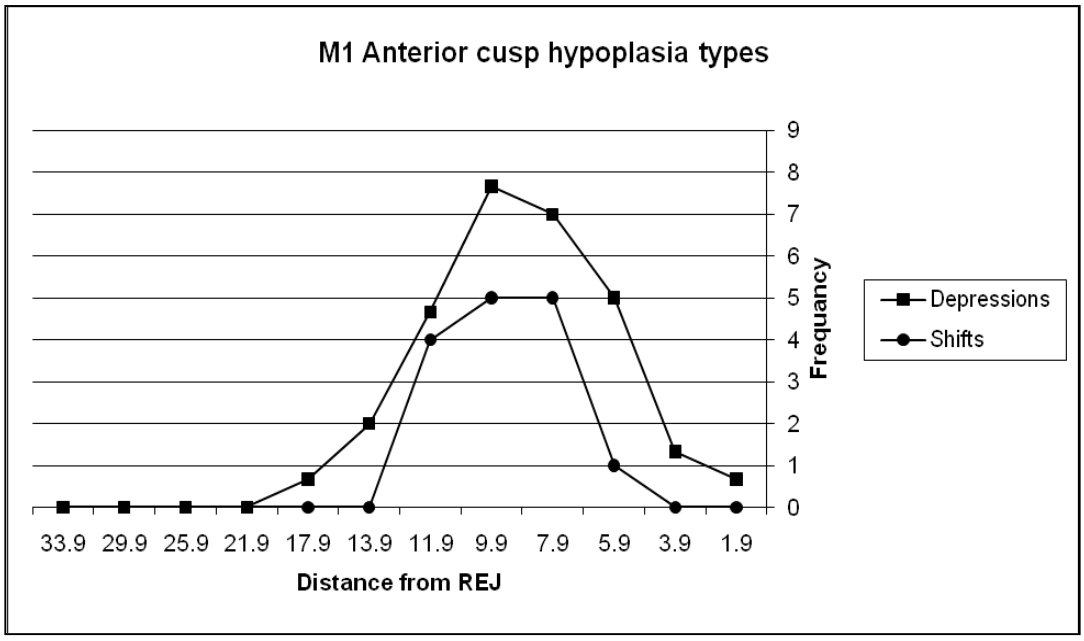

Figure 5.15: Relationship between 'shifts' and depression-type dental defects on the anterior cusp of the first molar in the North Ronaldsay population (shown as a running mean). Shift type defects are measured as depression-type defects - vertically up the centre of the cusp from the REJ to the central point of the anterior / posterior portion of the shift defect.

5.5.4 Defect severity

For the reasons outlined in the previous section, only defect severity data from the North Ronaldsay population are included in this analysis. Line-type hypoplastic defects were scored according to their severity and the frequency of the different severity scores plotted against crown development, shown in Figure 5.23. As with the other graphs investigating the seasonality of dental defect occurrence, identical adjustments taking into account the variation of growth down the tooth crown have been made and the data are plotted as relative frequencies of the total number of hypoplasias observed on each molar.

Figure 5.23 demonstrates that the most severe hypoplastic defects occurred during periods of key food shortages. The data also indicate that the more severe hypoplasias are present on the later developing teeth - with no severe enamel defects (score three or higher) found in the first molar and with score four defects only being identified in the third molar. The final months of development in the third molar would appear to be a particularly stressful time for the North Ronaldsay sheep, as both physiological and environmental stresses are acting upon them. Females would have just given birth to their first lambs during this period and subsequently, whilst lactating, would have been moved onto a terrestrial (copper rich) diet. This is also the period during which the animals suffer their greatest food shortages, due to the cessation of winter storms which would have provided abundant seaweed for them to eat. These multiple stress events occurring simultaneously, most likely explain the increase in frequency of more severe enamel hypoplasia observed by this study in later developing dentition.

However, there are perhaps other possible explanations for this increase in severe enamel hypoplasia in the lower portions of the enamel crown. As discussed previously in Chapter 4, the rate of enamel growth varies down the tooth crown, beginning rapidly at the apex of the tooth and then slowing down towards the lower portion of the crown. As the enamel formation rates slow down, the striae of Retzius

form a more obtuse angle with the dentine enamel junction. This decreases the amount of incremental plane exposed on the surface when enamel defects are formed, making them appear more delineated, and consequently more severe. As the third molar has the longest period of development, it also has the most slowly developing lower tooth crown segment, potential allowing more minor stress events to be manifested in the enamel as more moderate to severe enamel defects.

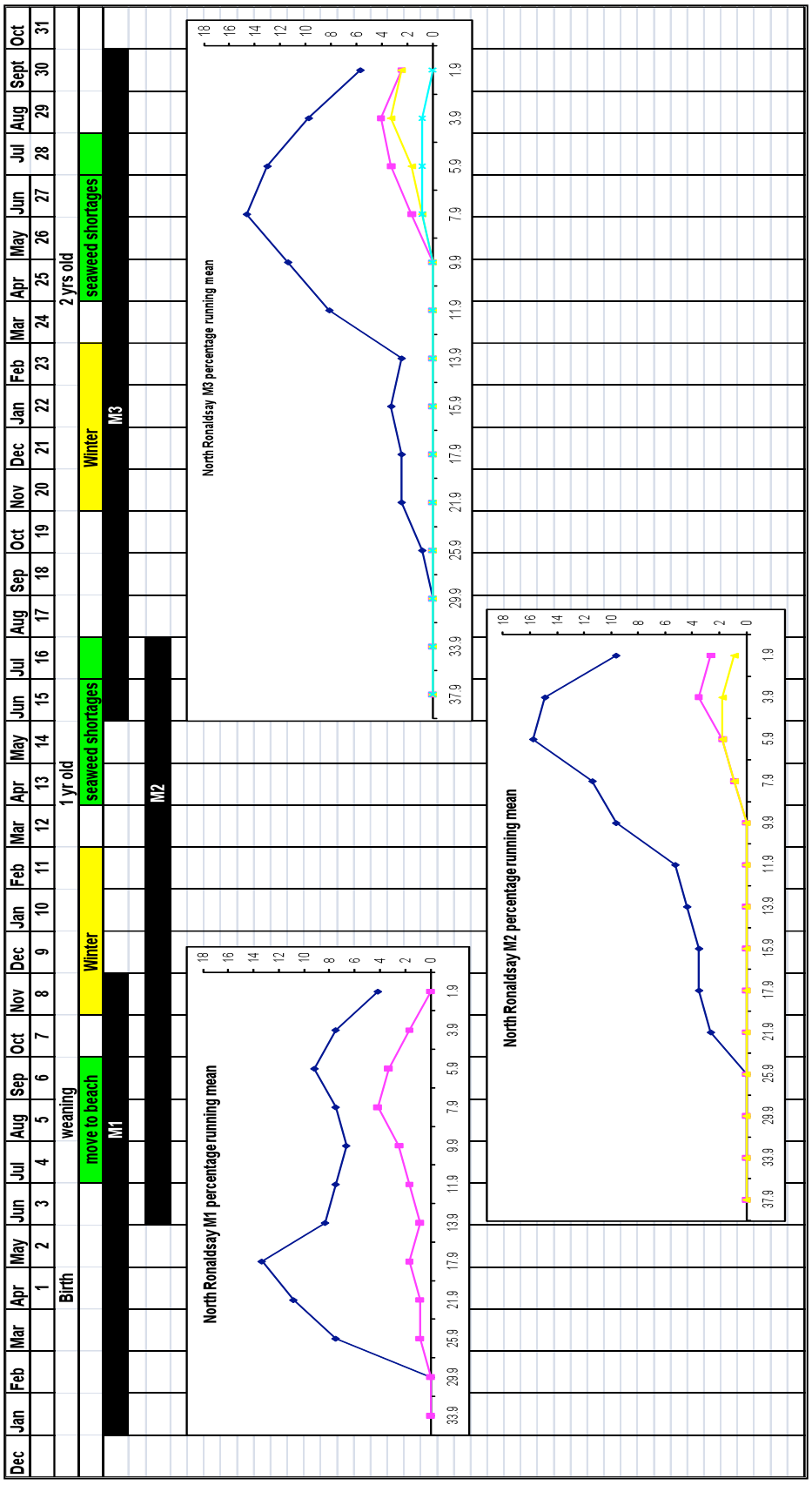

Figure 5.15: Showing the severity scores of enamel hypoplasia from North Ronaldsay plotted as percentage running means onto a chart of tooth development rates. Months after birth and physiological and dietary stressors are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present. Blue lines = Severity level 1, Pink lines = Severity level 2, yellow lines = severity level 3 and turquoise lines = severity level 4.

5.6 Conclusions

5.6.1 Identifying general levels of population stress

The data presented previously reveals that the challenging and rather unique environmental, physical and nutritional conditions facing the North Ronaldsay population are clearly reflected in higher levels of enamel hypoplasia when compared to the Hoy population. This supports the suggestions by Britt & Baker (1990) that the North Ronaldsay population are not as well adapted to their unusual environmental and dietary conditions as previously thought.

The very low frequency of enamel hypoplasia seen in the Skara Brae population is extremely interesting, and appears to suggest that this archaeological sheep population suffered less overall physiological stress than either of their modern counterparts on Hoy and North Ronaldsay. A similar low level of enamel defect occurrence in ancient sheep has previously been recorded at the Neolithic site of Papa Westray in Orkney (Balasse & Tresset, pers. comm.). This low level of enamel hypoplasia may be a reflection of different animal management strategies within these Neolithic populations, possibly relating to fodder provisioning over winter; alternatively it may also reflect higher biomass avalibility. It is suggested that at Skara Brae sheep may have had their winter fodder supplemented with seaweed, as identified at Papa Westray (Balasse, et al. 2006), meaning that at no periods were the animals under high levels of dietary stress. This lack of dietary stress in the Neolithic samples is in direct contrast to the modern datasets, which clearly both suffer periods of food shortages and associated nutritional difficulties.

All three of the Neolithic populations from Orkney (Skara Brae, Holm of Papa Westray and Knap of Howar) show lower levels of enamel hypoplasia than the two modern populations. These observed differences could relate to differences in animal

husbandry regimes, combined with factors such as climate change and biomass availability. The milder climate and reduced blanket peat levels in the Neolithic period would have meant that there was both more biomass and more grazing land available during the Neolithic period, potentially leading to less seasonal variation in grazing availability and decreased fodder provisioning pressure.

5.6.2 Seasonality

The occurrence of peaks in enamel hypoplasia (identified in both modern populations) around the time of birth and at five to six months after birth, clearly demonstrate the relationship between enamel hypoplasia and physiological stress events such as birth and weaning in caprine populations. The variation seen in the location on the tooth crown of enamel hypoplasia within the modern populations, and their apparent correlation with periods of nutritional stress brought about by periods of food shortages, reinforces the clear link in caprines between nutritional intake / food availability and the occurrence of enamel hypoplasia. This is also supported by the appearance of more severe hypoplasias during periods of food shortages.

5.6.3 Interpretation of defect types and severity

The underlying hypothesis that the type of stressor and its impact / duration is reflected in the different types and severities of hypoplastic defects is supported by the data from the North Ronaldsay population. The North Ronaldsay population faces more dietary and environmental challenges than the population from Hoy, and this is reflected in the higher percentages of severe types of defects (linear-type) and a higher percentage of defects with a high severity score.

When the different defect types from the North Ronaldsay population are plotted against the chronology of crown development, there are clear differences in the frequency distribution between lines and depression on the first and second molars. It

is possible that this is related to different seasonal stress events. However, similar distributions are not seen in the third molar and there is a close correlation in the distribution between depression-type defects and 'shift defects' in the crown produced during natural development. This may suggest that depression-type defects in high crowned species need to be treated with caution.

5.6.4 Summary & future work

This chapter has explored a range of baseline themes:

1) Identifying General Levels of Population Stress

The analyses presented in this chapter have clearly demonstrated that the occurrence of enamel hypoplasia can be used as a general marker of physical, nutritional and environmental stress in species with high crowned teeth. Sheep populations with more challenging environmental and physical conditions show higher levels of enamel hypoplasia and more severe defect types and severity levels. This indicates that enamel hypoplasia can be more confidently used as a general marker of stress within caprine populations, allowing broad reconstruction of animal management strategies in archaeological populations, potentially even including understanding fodder provisioning.

2) The seasonal occurrence of physiological events

Physiological stress events such as birth and weaning are also clearly visible in the enamel hypoplasia record on sheep teeth. This provides the first evidence to indicate that seasonally influenced physiological stress can be identified using enamel hypoplasia in caprine populations.

3) The impact of seasonal dietary variation

The data presented in this chapter has identified a clear correlation between seasonal variation in nutritional levels and increases in the occurrence of enamel hypoplasia in caprine teeth. Such a correlation will allow seasonal and dietary variation in ancient sheep remains to be further explored.

4) The Interpretation of Defect Types and Severities

The analysis of different types of defects and their severity scores has been demonstrated to be a useful tool in the assessment of general stress levels in caprine populations. However, care needs to be taken in the interpretation of dental defect types, particularly with regard to depression-type defects.

5) Future work

The time constraints imposed on the collection of material from Skara Brae meant that only a small sample of isolated teeth could be recorded, from only a limited number of contexts. In terms of future work, the analysis of the complete assemblage (ideally including the analysis of complete mandibles not just isolated teeth), would allow a more detailed picture of the animal husbandry practices at this site to be drawn.

Continued investigations into the different types of defects and their severities - in relation to different forms of stress events - is also an area for future study. Data presented in this chapter has clearly demonstrated their potential links to seasonal / physiological events and more detailed investigations into populations with more tightly defined/known seasonal and physiological stress profiles would be of great interest. Further investigations could be carried out using thin section techniques to explore histology similar to that carried out by Witzel, et al. (2006) in relation to humans. It is also of great importance that more research is undertaken into

depression-type defects in high crowned species and their possible link to natural developmental abnormalities.

6 Modern and archaeological caprines from Kenya

This chapter provides the second of three, comparative geographically specific case studies investigating the application of the methodology developed in Chapter 4 and the interpretation of enamel hypoplasia in modern and ancient caprine populations. Two data-sets are explored: The first is a collection of modern sheep and goats from south west Kenya analysed to investigate the relationship between the occurrence and severity of enamel hypoplasia and differing environmental factors related to topography and ecology. Analysis of (and interpretation of preliminary results from) the modern datasets was carried out in close collaboration with Dr Marie Balasse (Centre National de la Recherche Scientifique, Paris) and is already the subject of a publication (see Balasse, Upex and Ambrose, in press and Appendix 1). Consequently, the findings of this paper will only be briefly summarised at the beginning of this chapter. Further research during this thesis has, however, re-examined these modern data and new findings will be discussed in more detail. The second dataset derives from a number of archaeological sites from the same southwest region of Kenya as the modern sample, dating from the early Neolithic period through the development of pastorialism in the region.

6.1 Introduction

Kenya is situated astride the equator on the east coast of Africa. To the north, the country is bordered by Sudan and Ethiopia, with Uganda to the west and Tanzania to the south. The country has approximately 500 kilometers of coast line on the Indian Ocean and covers an area of around 583,000 square kilometers (Mathu & Davies,1996). Kenya is divided by the Great Rift Valley which runs through the country. The rift consists of a 50 – 70 kilometer wide fissure that extends from Lake Turkanna in the north, right down through the centre of the country, at times reaching depths of 600 to 900 meters below the surrounding land (Mathu & Davies, 1996). This massive geological feature produces a great deal of regional environmental diversity within the country.

Kenya is situated within the Inter-Tropical Convergence Zone (ITCZ); this produces an unusual pattern of rainfall in the country, characterized by two wet seasons: March to early June and late October to early December (Davies, et al. 1985). Approximately 83 % of the country is located in arid or semi- arid regions which have suffered from long term degradation. Major droughts occur in these regions every decade and minor droughts every three to four years, with obvious consequences for the nutritional and health status of domestic livestock (UNEP/GoK, 2000; Orindi, et al. 2007; Lasage, et al. 2008; Speranza, et al. 2008, Balasse, et al. in press). While the local pastoralist groups have adapted to these droughts and the unpredictable nature of the arid regions, they still affect a large number of livestock (Ryan, et al. 2000; Orindi, et al. 2007; Mworia & Kinyamario, 2008, Balasse, et al, in press).

6.1.1 Summary of the modern Caprine material

The modern material was recorded and analysed following the methodology discussed in Chapter 4 as part of a collaborative project with Dr Marie Balasse. The preliminary findings are published (Balasse, et al. in press) and subsequently only briefly discussed below. The paper is included as Appendix 1.

In June and July 2000, 2001 & 2002 M. Balasse and S. Ambrose collected 116 molars from 56 domestic sheep and goats from the semi-arid Narok South region and the more mesic Central Rift Valley region of south western Kenya. Of the 56 animals collected, there were 23 sheep, 23 goats and 10 that were unidentified (some animals were purchased by the team, the other samples were collected from rubbish deposits and identified to species morphologically (see Appendix 1 and Chapter 4 for more details on the morphological methods used in the separation of sheep and goats in this material). In the year 2000 there was a severe drought in Kenya, caused by the failure of four consecutive rainy seasons over two years. Three key issues were investigated in this paper: 1) The ability to separate sheep and goats in the material using morphological features identified by Balasse and Ambrose (2005b) provided an ideal opportunity to investigate whether the two species responded differently to environmental pressures such as drought, in terms of the formation of enamel defects; 2) As many of the animals were between two and three years of age at death, the severe drought that occurred in 2000 should have potentially been recorded in the occurrence and severity of enamel hypoplasia, allowing the impact of severe climatic / environmental variation to be studied; 3) The two different environmental regions studied (the semi-arid Narok South region and the more mesic Central Rift region) allowed an investigation into the impact of regional environmental variation on the occurrence and severity of enamel hypoplasia.

The work by Balasse, et al. (in press) revealed several significant results: 1) We demonstrated that the semi-arid Narok South region had a statistically higher frequency of hypoplastic defects and that these defects were significantly more severe than those from the more mesic region. 2) We also demonstrated that sheep had a higher percentage of enamel hypoplasia in the Central Rift Valley than was found in goats, although when all caprines from both regions were compared, sheep were not statistically different from goats. 3) Interestingly, the severe drought of 2000 was not visible in the data - although it is suggested that this is perhaps due to the small data-set and associated methodological problems. The preliminary modern data also did not reveal any obvious patterns of seasonality in the distribution of hypoplasia on the tooth crown. The paper suggested that this was due to a lack of

seasonality of birth in this region, causing seasonal events to affect animals of various ages, producing hypoplastic defects at different developmental points in the teeth (Balasse, et al. in press: 12)

This preliminary work on modern Kenyan caprine enamel hypoplasia concludes that as the difference in hypoplasia severity and frequency between the two environmental regions is not explained by differences in either the proportions of species (sheep and goat), or the ratio of indigenous to exogenous breeds, it must be 'seen as a reflection of the more fragile balance of the herding system in the arid climate compared to the more mesic climate of the Rift Valley' (Balasse, et al. in press: 14). The difference between sheep and goats in the Rift Valley is further explained by both feeding behaviour and resistance to disease. We suggest that a preference for grazing in sheep and browsing in goats implies that goats would be less affected by the rarefaction of grassy resources in drought periods. Other possible causes of hypoplasia are discussed including intestinal and respiratory diseases, which affect both species in Kenya. However, goats are reportedly more resistant to these infectious diseases than sheep, potentially also leading to an increase in the occurrence of hypoplasia in sheep. It is suggested that the difference between the species is not visible in the Narok South data-set due to the small sample size (see Balasse, et al. in press and Appendix 1 for more details).

6.1.2 The archaeological caprine material

In order to provide a comparative temporal framework for the modern caprine data from Kenya, archaeological material was selected from two of the varied regional sub-cultures present in Kenya in the early Neolithic period (approximately 3000-2000 BC Robertshaw, 1990). Elmenteitan (ELM) and Savannah Pastoral Neolithic (SPN) sites are both characterized by faunal assemblages heavily dominated by domestic animals (Gifford-Gonzalez & Kimengich, 1984; Gifford-Gonzalez, 1985; Marshall, 1990a; 1990b). The domination of domestic mammals, combined with the limited archaeological evidence of agricultural practices found on these sites, suggests that these Neolithic communities had adopted a specialized pastoral

economy (Marshall, 1990a; 1990b; Gifford-Gonzalez, 1998, 2000). The two cultures are compared in Table 6.1.

Two different types of site were also selected for study: open area savannah sites and rock shelter sites (for a summary of the sites selected see Table 6.2). The open savannah sites are located in the Loita-Mara plains and the Narok South region of Kenya, while the rock shelter sites are found in the Central Rift Valley and the Mau Escarpment (See Figure 6.1). These two different types of site were selected because it was expected that their different environmental locations would be reflected in the enamel hypoplasia signatures of caprines.

The Loita-Mara plains region of south west Kenya contains high numbers of archaeological sites. The region is bounded to the west by the Soit Ololol escarpment, to the east by the Loita Hills, to the south by the Kenyan border with Tanzania and to the north by the Amala and Ewaso Ng'io rivers and forests of Mau. It is a region of high elevation within Kenya, ranging between 1700-1900 metres above sea level. The area consists of open plains dissected by mara drainage systems and ranges of quartzitic hills. The distribution of Neolithic sites in this landscape shows many similarities with modern pastoral villages. Settlements are situated on gentle slopes favouring soil drainage and share a similar structural layout to modern settlements (Robertshaw, 1990; Marshall, 1990a).

	Elmenteitan	**Savannah Pastoral Neolithic**

Dates	3000 – 1200 BP - Appears to supplant SPN culture in western Kenya.	4000 – 1200 BP - Begins in the north and spreads southwards
Location of occupation sites	Rock shelters and open plain sites.	Open savannah sites.
Trade links	Extensive evidence for trade and exchange.	Limited evidence for trade and exchange.
Re-use of previously occupied sites	Common, often associated with high artefact density.	Rare, with low densities of artefacts.
Economy	Pastorialism, almost exclusively based on cattle, sheep and goats.	Mixed, mainly pastoral, but some sites with high levels of wild fauna.

Table 6.1 : The key differences between the Kenyan Neolithic cultures.

Site	Culture	Environment / Location	Site type	Fauna
Lemek North East	SPN	Semi Arid / Narok South	Open Plain	Entirely domestic, Caprine dominate
Narosura	SPN	Semi Arid / Narok South	Open Plain	Mainly domestic, Caprine dominate
Enkapune Ya Muto	ELM	Mesic / Mau Escarpment	Rock shelter	Mainly domestic, Caprine dominate
Ngmuriak	ELM	Semi Arid / Narok South	Open Plain	Mainly domestic, 52% Caprine

Table 6.2 : Comparison of the Kenyan Archaeological sites.

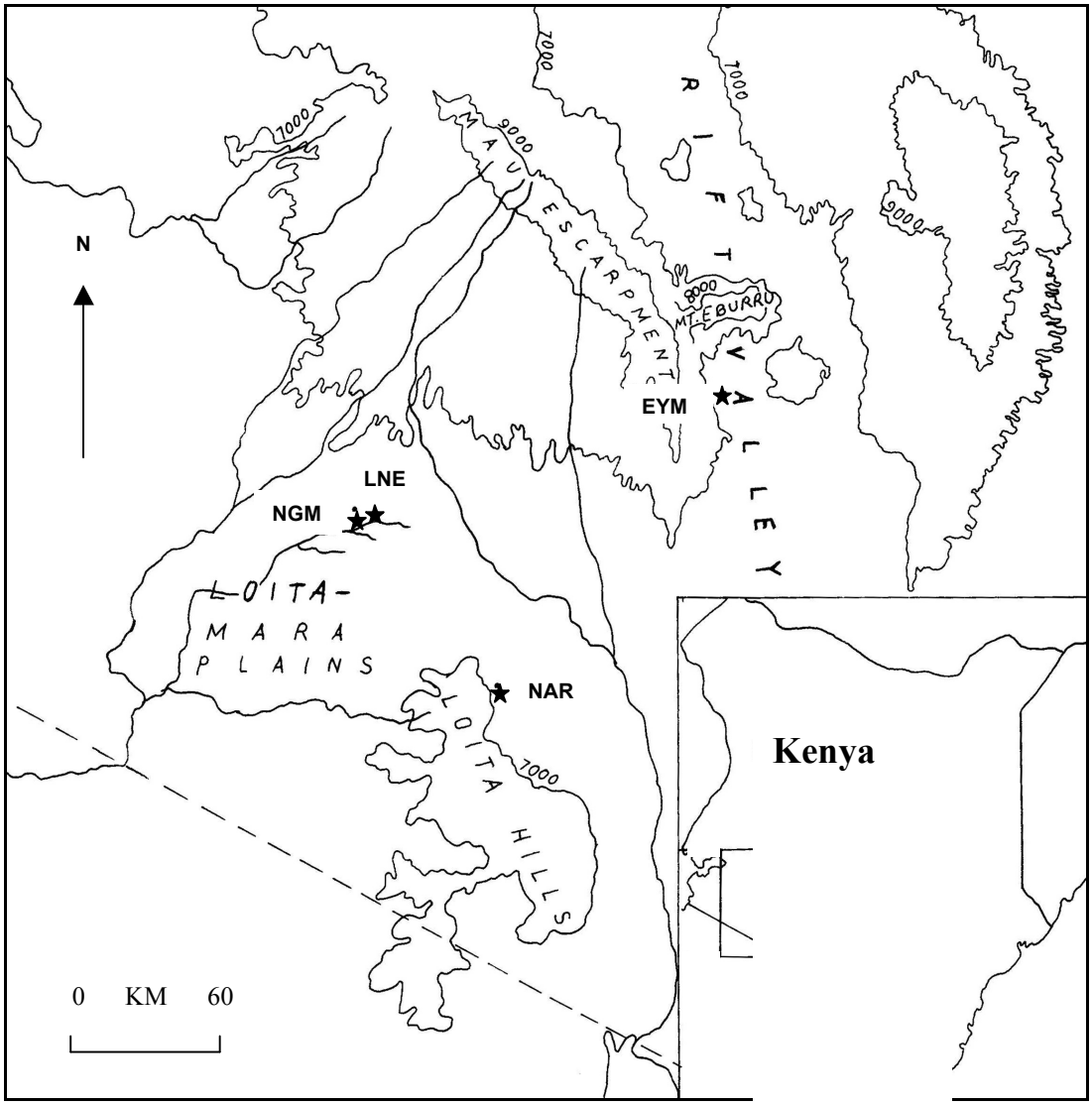

Figure 6.1: The location of the Kenyan archaeological sites included in this study from the Loita – Mara plains and the Mau escarpment. NAR = Narosura, NGM = Ngmuriak, LNE = Lemek North East, EYM = Enkapune Ya Muto.

In the Central Rift Valley, Elmenteitan groups intensively settled and occupied small rock-shelters, previously sporadically occupied by Eburran-5 hunter-gatherers. These rock-shelters on the eastern side of the Mau escarpment contrast greatly with the larger open settlements of the Loita-Mara plains in two key ways: The first is their location in a variety of habitats from open Savannah to forested environments, and the second is the higher proportions of wild animal remains in the faunal assemblages than in those from the Loita-Mara plains sites (Ambrose, 1995).

Gifford-Gonzalez (1985) has previously stated that the occurrence of enamel hypoplasia in caprines was higher in the Elmenteitan rock-shelter site of Maasai Gorge than the Savannah Pastoral Neolithic assemblage from Narosura (unfortunately the Maasai Gorge site was unavailable for study as part of this research). She postulates this could be due to differences in herding practices between the different cultures (Gifford-Gonzalez & Kimengich, 1984; Gifford-Gonzalez, 1985). Marshall (1990a) also reported a 6.3% incidence of enamel hypoplasia in the caprine assemblages of Ngmuriak (Elmenteitan) and a slightly lower frequency in the smaller assemblage of Lemek North East (Savannah Pastoral Neolithic). These early studies, combined with archaeological evidence, have been used to suggest that the different types of sites could have had slightly different animal management and pastoral strategies (Robertshaw, 1988).

6.2 Background to the archaeology of the region and the sites studied

The earliest patterns of subsistence in the East African Neolithic indicate a diverse subsistence base, including hunting, fishing, herding and agriculture, which appears to have been practiced from around 4,000 BP (Marshall, 1990b). By about 2,600 BP this broad subsistence base appears to have shifted in favour of a more specialised pastorialism, focused on the production of food purely from domestic herds, with the exclusion of almost all wild resources. While there are many economic, social and ecological factors which must have affected this shift in subsistence patterns, it has been suggested that a change in the rainfall patterns in Eastern Africa may have been one of the key factors (Marshall, 1990b).

6.2.1 The Savannah Pastoral Neolithic (SPN)

The Savannah Pastoral Neolithic takes its name from the preference for site locations in the open savannah regions of East Africa and the strong emphasis on pastoral subsistence strategies. According to Ambrose (1991) the absolute time period of this culture is from 5,000-1,200 BP. However, domesticated livestock are not present in the assemblages before 4,000 BP and there are no sites in the highlands before 3,300 BP. The earliest dated sites are all located in the Turkana Basin in Northern Kenya and it is suggested that the slow development of adaptations to tropical diseases in the domestic animals may have slowed the spread of pastorialism from the North of the region down into the more tropical Southern Highlands (Gifford-Gonzalez 2000). The earliest phases of SPN in the highlands are closely associated with the occurrence of Eburran-5 microliths, suggesting a long period of sporadic contact with these local highland hunter gatherers before the pastoralist expansion into the south. Two sites were chosen from the SPN period to be included in this analysis; both had moderately large faunal assemblages with good preservation.

Lemek North East (LNE)

This site is located in the Lemek valley (semi-arid region of Narok South) in an area of open Savannah. At 1980 metres above sea level, it is one of the highest archaeological sites in the region. The site consists of a midden including SPN artefacts, with a radiocarbon date of 2225 ± 140 ^{14}C BP. The faunal assemblage is exclusively composed of domestic animals, among which caprines predominate over cattle in absolute numbers (Marshall & Robertshaw, 1982; Marshall, 1990a).

Narosura (NAR)

The site of Narosura is located in the Loita Plains (semi-arid region of Narok South), in an area of open Savannah. The site consists of a long term settlement occupied by SPN communities, from between 2760 ± 115 ^{14}C BP to 2360 ± 110 ^{14}C BP. The faunal assemblage is heavily dominated by domestic animals, with cattle outnumbering caprines (Gifford-Gonzalez & Kimengich, 1984).

6.2.2 The Elmenteitan Neolithic (ELM)

The Elmenteitan culture is found in the highlands of western and south-western Kenya, and the Loita-Mara plains to the west of the Rift Valley from between 3,000 – 1,200 BP (Ambrose, 1991). Like the SNP many of the Elmenteitan settlement sites are located in open Savannah regions and appear very similar to modern day pastoral villages because of their lay-out and situation. However, in the central rift valley region, Elmenteitan groups intensively occupied rock shelter sites previously occupied by the Eburran 5 hunter gathers. The earliest Elmenteitan sites are found on the Mau escarpment dating to around 3,000 BP, with later sites appearing in the south of the region around 2,500 BP. Although the Elmenteitan and the SPN are both found in western and south-western Kenya, the Elmenteitan is chronologically younger and appears to expand southwards into the regions occupied by the Savannah Pastoral Neolithic people (Ambrose, 1991).

The material culture of the two groups are almost never found at the same sites (even though there is a clear temporal and spatial overlap in their occupation) suggesting that there was little interaction between them (Ambrose, 1991). Unlike the SPN people, there also appears to have been very little interaction between the Elmenteitan culture and the local hunter-gatherer Eburran-5 cultures. However, the Elmenteitan sites do have much high proportions of traded obsidian and pottery. This local exchange network appears to have been much stronger than that of the SPN and suggests that the Elmenteitan culture may have had much stronger regional, political and military integration. It is suggested that this may have facilitated their territorial expansion and the replacement or absorption of SNP groups in south-western Kenya (Ambrose, 1991).

Three sites from this period were selected for study; two rock shelter sites and an open plain site. Unfortunately it was discovered that the faunal remains from one of the rock shelter sites (Maasai Gorge) was unavailable for study and the one remaining rock shelter site (Enkapune Ya Muto) only contained a very small number of teeth suitable for study, making the comparison of rock shelter sites and open plain sites for this period difficult.

Enkapune Ya Muto (EYM)

The site of Enkapune Ya Muto is located in the mesic habitat of the Mau escarpment in an ecotone of forest/Savannah at an elevation of approximately 2400 m. The site consists of a rock-shelter extensively occupied from Middle Stone Age until Iron Age period (Ambrose, 1998). Occupation by Eburran-5 groups starts at the beginning of the 5th millennium BP. The first domestic fauna from the site date to 3990 BP and consist exclusively of caprine remains. Cattle are present around 3390 BP, in a faunal assemblage that was largely dominated by small wild bovids (Marean, 1992, Ambrose, 1998). The Elmenteitan culture appears at the site around 2600 BP. Preliminary study of the Elmenteitan faunal assemblage indicates it is mostly composed of domestic species, among which caprines dominate over cattle (Ambrose, 1984b). The tooth assemblage from this site is small: EYM is unusual in

having very poor teeth preservation, probably due to a post-depositional agent (Marean, 1992).

Ngmuriak (NGM)

Ngmuriak was discovered in 1980 in the Lemek Valley (semi-arid region of Narok South) in a region of open savannah. It is a relatively short term occupation site settled by Elmenteitan pastoralists. The site covers an area of approximately 8250 square metres of gently sloping hillside at an elevation of approximately 1900 metres and was extensively test pitted with some areas being opened up for further excavation. Archaeological remains were uncovered at 40cm below the ground surface and all the faunal remains were contained within in one band of dark brown silty soil 20-30 cm deep, lying along the line of the modern hillside (Marshall & Robertshaw 1982). The large bone assemblage includes 98% domestic remains, of which 52% are caprines (Marshall, 1990a). Possible models for Elmenteitan pastoral strategies in this region range from transhumance between the Lemek valley and higher elevations, with dry season grazing taking place on the Mau escarpment, to relatively settled communities in the Lemek valley with occasional stock movement during drought periods to the Mara river. The latter of these strategies is currently practised by the Maasai living in this region.

6.3 Key Research Themes

Interpreting animal husbandry practises

This theme follows on from the conclusion in the proceeding chapter that enamel hypoplasia can be used as a general stress indicator in caprine populations. In this chapter this concept is developed and used to compare the archaeological sites, exploring the relative frequency, type and severity of enamel hypoplasia, their variation between sheep and goats and between different site types and cultures. Two principal questions are addressed using data from enamel hypoplasia:

1) Are there differences between the two cultural groups (i.e. Elmenteitan and the Savannah Pastoral Neolithic cultures) in terms of their animal management strategies?

2) Are there differences between the types of sites studied (i.e. open air sites and rock shelter sites).

Investigating differences between sheep and goats

The opportunity in these archaeological populations to separate sheep from goats gives rise to the second research theme addressed in this chapter. This investigates differences potentially caused by variation in the diet of these two species. It is expected that the differences seen would be very similar to those identified by Balasse, et al (in press). Any other variations seen between sheep and goats in terms of the frequency, severity and type of enamel hypoplasia should reflect variation in archaeological animal management strategies in comparison with the modern material studied.

Identifying and interpreting seasonality

The final theme addressed in this chapter is again, one which runs throughout the thesis – i.e. using both the archaeological and modern material from Kenya to

investigate the potential of caprine enamel hypoplasia in unravelling seasonal signatures past and present. Two different aspects of seasonality are explored by using the distribution of enamel hypoplasia on the tooth crown:

1. *Seasonality within physiology and animal husbandry*: Data discussed in the previous chapter revealed that physiological events such as birth and weaning produce a signature within the distribution of enamel hypoplasia on the tooth crown. This is further developed within this chapter and used to study the signatures of birth and weaning in archaeological populations with unknown management strategies.

2. *Climatic seasonality:* the second aspect of seasonality to be investigated is the impact of climatic seasonality throughout the year and its impact on the frequency of enamel hypoplasia. This aspect of seasonality studies the potential of enamel hypoplasia to be used as a marker for seasonal environmental or climatic changes in archaeological populations.

6.4 Results

A total of 381 recordable teeth were analysed from the archaeological sites, of which 267 showed hypoplasia. The number of teeth recorded at each site varied greatly, depending on the size and preservation at each: 193 teeth were recorded from the site of Ngmuriak; 107 from Narosura; 52 from Lemek North East and just 29 from Enkapune Ya Muto. In all four populations the number of identified goat molars outnumbered those of sheep. The data showing the relative percentage frequency of different caprine species at each site is shown in Table 6.3.

Site	Sheep	Goat	Unidentified
Ngmuriak (n=193)	31 %	65 %	4 %
Lemek North East (n=52)	23 %	77 %	0 %
Narosura (n=107)	33 %	55 %	12 %
Enkapune Ya Muto (n=29)	45 %	55 %	0 %

Table 6.3: The percentage of total molars identified to each species at Kenyan archaeological sites.

6.4.1 Interpreting animal husbandry practises

Key points

- Enkapune Ya Muto has a statistically higher frequency of enamel hypoplasia compared to the other archaeological sites ($\chi^2 = 0.007$).
- Goats at Enkapune Ya Muto statistically have more enamel hypoplasia than sheep ($\chi^2 = 0.008$).
- Goats at Enkapune Ya Muto statistically have more sever defects than goats at open plain sites ($\chi^2 = 0.001$), but there is no difference between sheep at this site and sheep at the open plain sites.

General results

The archaeological material from the three large open plain sites shows similar levels of enamel hypoplasia to those found by Balasse, et al. (in press) in modern samples, with between 67-79% of all tooth crowns showing enamel defects. The relative frequency of tooth crowns showing enamel hypoplasia is 93% from Enkapune Ya Muto, 67% from Ngmuriak, 79% from Lemek North East and 70% from Narosura (See Figure 6.2 and Table 6.4)

The frequency of enamel hypoplasia is considerably higher at the site of Enkapune Ya Muto than at the other three sites and this difference is statistically significant ($\chi^2 = 0.007$). Goats at the rock shelter site of Enkapune Ya Muto have a statistically higher frequency of enamel hypoplasia than the sheep from this site ($\chi^2 = 0.008$) see Figure 6.2. Goats at this site also have a statistically higher number of severe linear hypoplasias than goats at the open plain sites ($\chi^2 = 0.001$). While sheep at Enkapune Ya Muto do have a slightly higher number of enamel hypoplasias when compared to the animals from the open plain sites, this difference is not statistically significant. No significant differences were identified either between the species or in total when the frequencies, severity or types of enamel hypoplasia are compared for the two different cultural groups (Figure 6.3, Table 6.5 and Figure 6.4, Table 6.6).

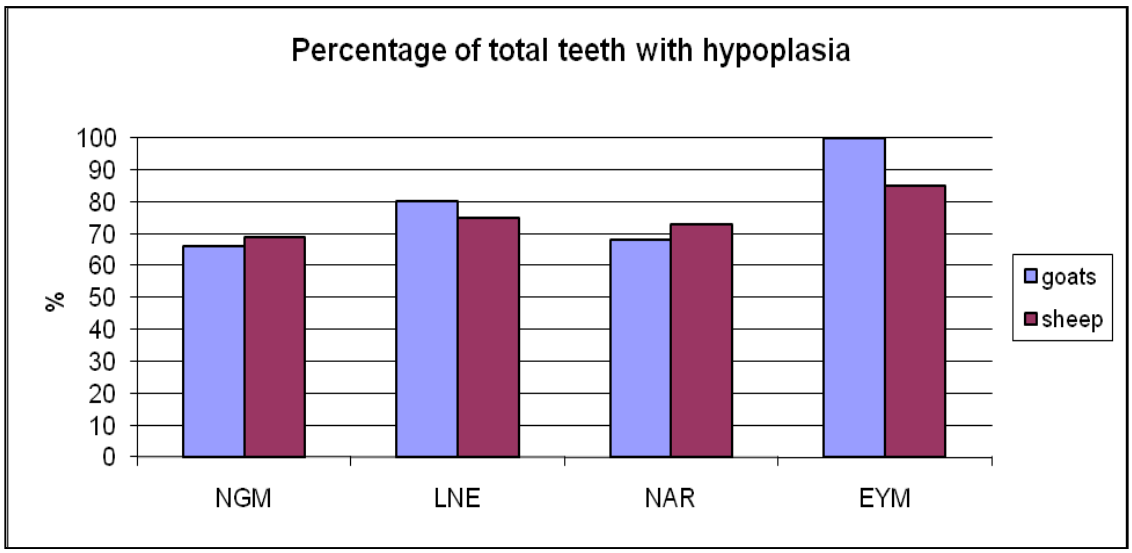

Figure 6.2: The percentage relative frequency distribution by species at Kenyan archaeological sites (NGM = Ngmuriak, LNE = Lemek North East, NAR = Narosura, EYM = Enkapune Ya Muto).

	NGM	LNE	NAR	EYM
Total no. complete teeth	193	52	107	29
No. teeth with hypoplasia	130	41	75	27
% of total complete teeth with hypoplasia	67%	79%	70%	93%
Total no. complete sheep teeth	59	12	48	13
No. Sheep teeth with hypoplasia	41	9	35	11
% of compete sheep teeth with hypoplasia	69%	75%	73%	85%
Total no. complete goat teeth	125	40	59	16
No. goat teeth with hypoplasia	83	32	40	16
% of compete goat teeth with hypoplasia	66%	80%	68%	100%

Table 6.4 : Comparison of the raw data and relative frequencies of enamel hypoplasia between archaeological sites and species. (NGM = Ngmuriak, LNE = Lemek North East, NAR = Narosura, EYM = Enkapune Ya Muto).

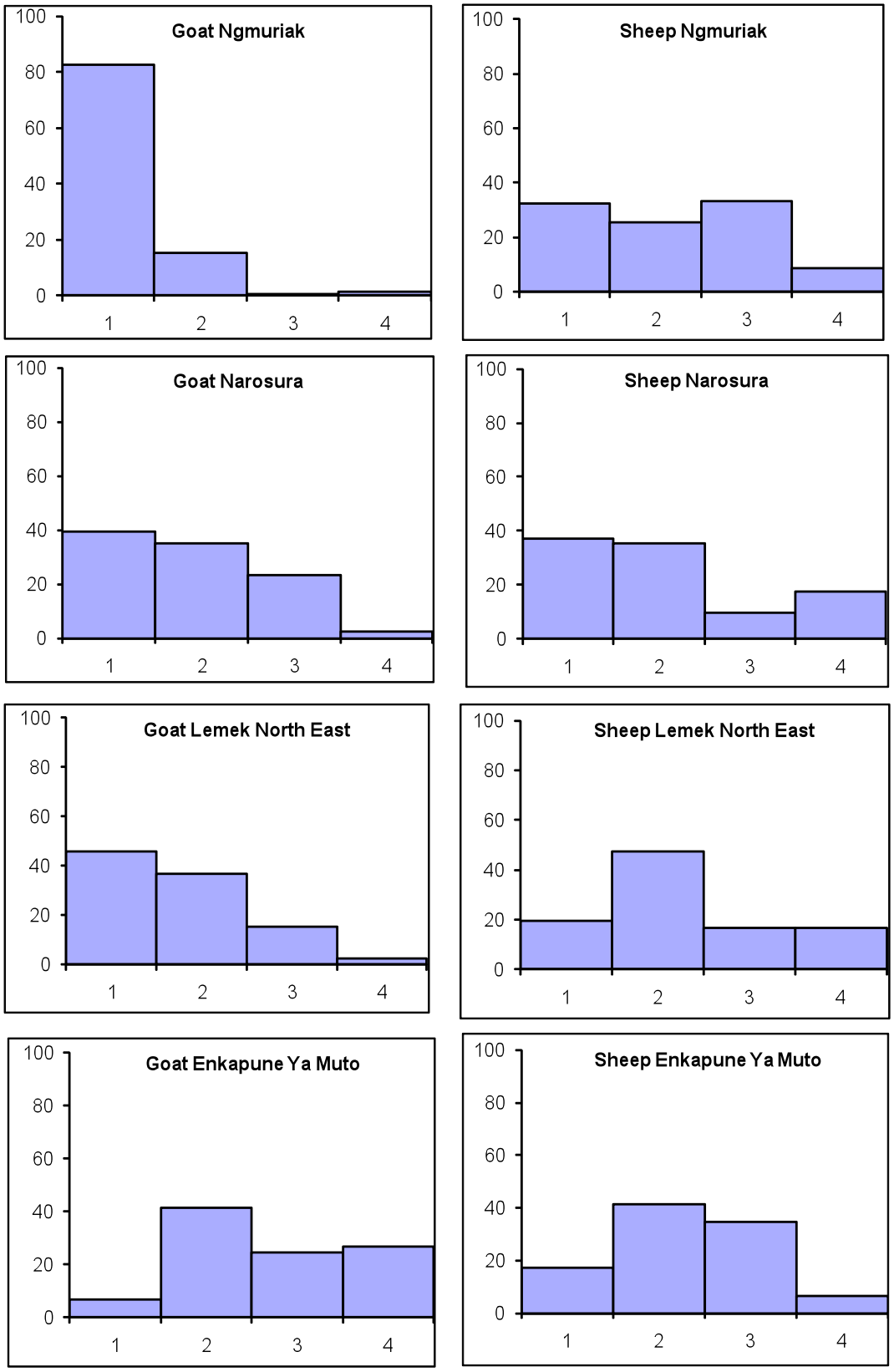

Figure 6.3: The relative frequency of defect severity scores (1 to 4) for each species at Kenyan archaeological sites.

Severity Score Goats	1	2	3	4
hypoplasia Narosura Capra (n=43)	40%	35%	23%	2%
hypoplasia Enkapune Ya Muto Capra (n=98)	7%	42%	25%	27%
hypoplasia Ngmuriak Capra (n=183)	83%	15%	1%	1%
hypoplasia Lemek North East Capra (n=64)	64%	25%	10%	1%
Severity Score Sheep	**1**	**2**	**3**	**4**
hypoplasia Narosura Ovis (n=51)	37%	35%	10%	18%
hypoplasia Enkapune Ya Muto Ovis (n=46)	17%	41%	35%	7%
hypoplasia Ngmuriak Ovis (n=182)	32%	25%	33%	9%
hypoplasia Lemek North East Ovis (n=36)	28%	43%	15%	15%

Table 6.5 : Relative frequency of enamel hypoplasia recorded for each severity score in sheep and goats from Kenyan archaeological sites

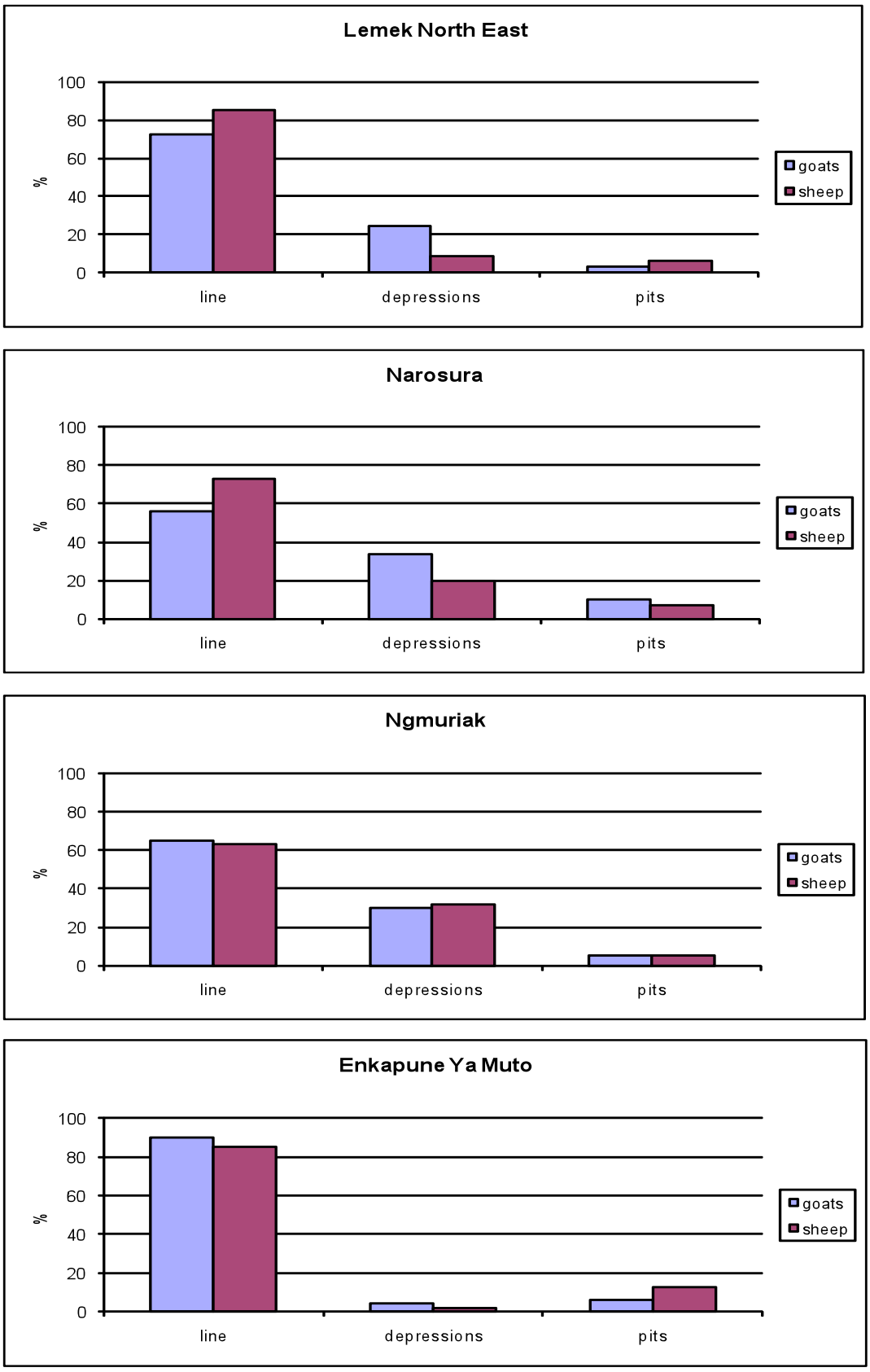

Figure 6.4: Comparing the relative frequency of different types of hypoplasia between species at Kenyan archaeological sites.

Defect Types Goats	**Lines**	**Depressions**	**Pits**
hypoplasia Narosura Capra (n=77)	56%	34%	10%
hypoplasia Enkapune Ya Muto Capra (n=99)	90%	4%	6%
hypoplasia Ngmuriak Capra (n=213)	56%	30%	5%
hypoplasia Lemek North East Capra (n=95)	73%	24%	3%
Defect Types Sheep	**Lines**	**Depressions**	**Pits**
hypoplasia Narosura Ovis (n=70)	57%	20%	7%
hypoplasia Enkapune Ya Muto Ovis (n=54)	85%	2%	13%
hypoplasia Ngmuriak Ovis(n=161)	63%	32%	5%
hypoplasia Lemek North East Ovis (n=47)	85%	9%	6%

Table 6.6 : Comparing the relative frequency of enamel hypoplasia recorded for each defect type between sheep and goats and Kenyan archaeological sites.

6.4.2 Investigating differences between archaeological sheep and goats

Key Points

- There is no overall difference between sheep and goats in terms of the frequency of enamel hypoplasia
- Sheep have more severe defects (score 2,3 & 4) than goats
- There is no overall difference between sheep and goats in terms of the types of defects recorded

General Results

The separation of sheep and goat was carried out using the methods described in Chapter 4, with a focus on the two key traits described by Balasse and Ambrose (2005b). Most of the archaeological material showed clear differences between the two species, with the most obvious difference being the narrowing of the mesial face towards the occlusal surface (See Figure 6.5). Only heavily worn crowns could not be separated.

Figure 6.5: The clear morphological differences between sheep and goat in the Kenyan archaeological material (goat on the left, sheep on the right).

There is no overall statistical difference in the frequency of enamel hypoplasia between sheep and goats. However, when the total severity levels for all sites are compared, sheep have a higher proportion of severe defects (Figure 6.6 and Tables 6.7 & 6.8). Goats also show a slightly higher relative frequency of depression type hypoplasias compared to sheep (see Figure 6.7 and Tables 6.7 & 6.8). A re-analysis of the modern material studied by Balasse, et al. (in press) showed a highly significant difference in the distribution of defect types between the species (χ^2 = 0.001) with goats having higher frequency of mild impacts (depression and pits) compared to sheep (Figure 6.8, Table 6.9). However, none of the differences noted in the archaeological material were statistically significant. No differences were noted between sheep and goats in terms of the distribution of defects on the tooth crowns.

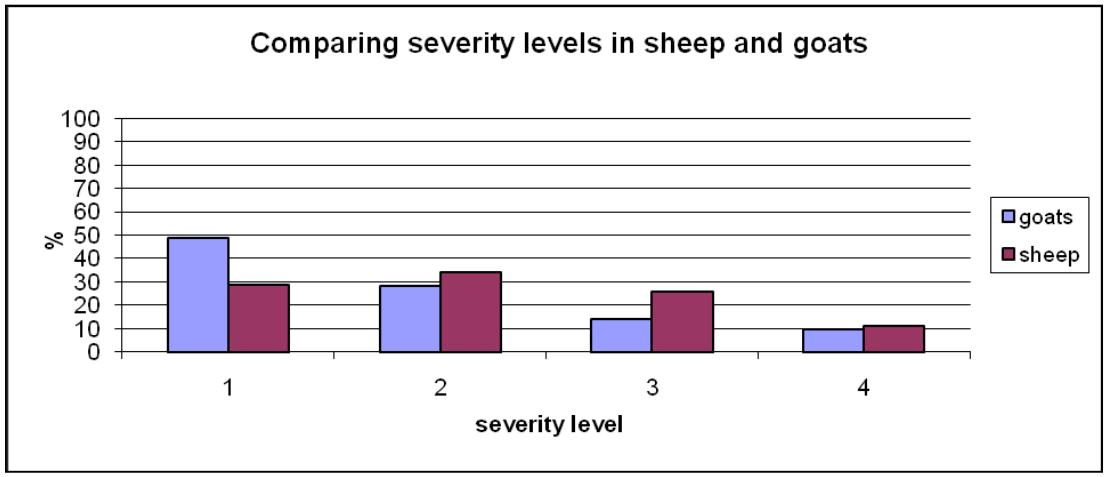

Figure 6.6: The relative frequency of total enamel hypoplasia defects in each severity level from all Kenyan archaeological sites.

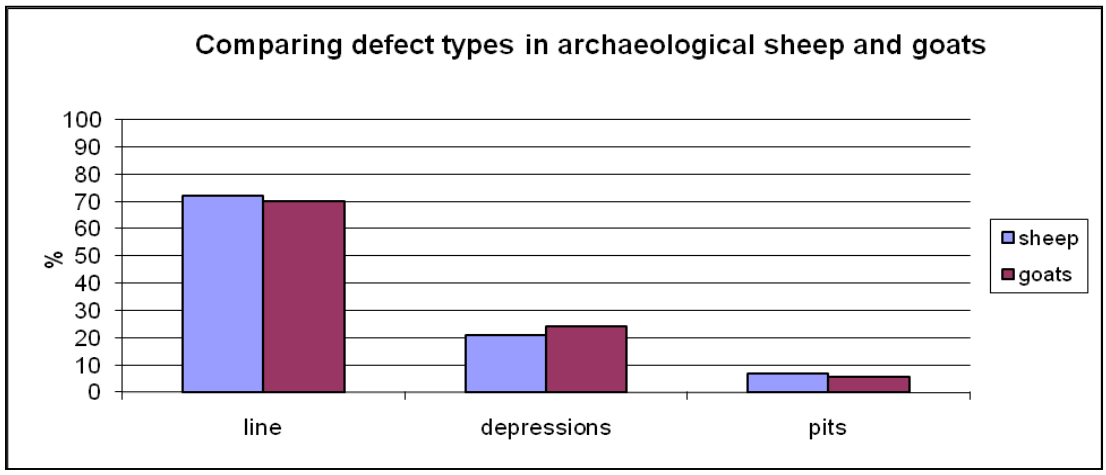

Figure 6.7: The relative frequency of each defect type from all Kenyan archaeological sites.

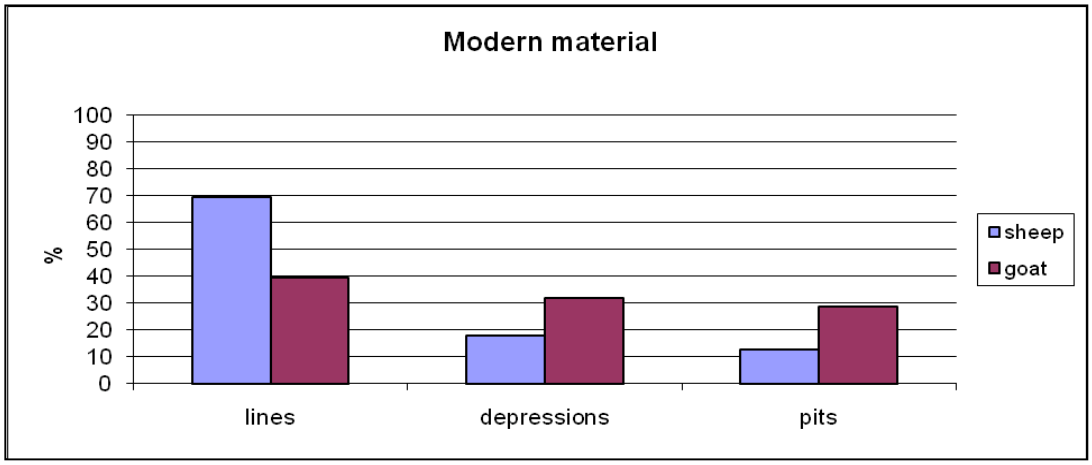

Figure 6.8: The different types of hypoplasia between species in the modern Kenyan material.

% total hypoplasia per species	Goats (n=348)	Sheep (n=232)
% hypoplasia in severity score 1	49%	29%
% hypoplasia in severity score 2	28%	34%
% hypoplasia in severity score 3	14%	26%
% hypoplasia in severity score 4	9%	11%

Table 6.7 : Relative frequency of enamel hypoplasia recorded per species in terms of defect severity.

% total hypoplasia per species in archaeological data	Goats (n=484)	Sheep (n=332)
%. Line type hypoplasia	72%	70%
% Depression type hypoplasia	21%	24%
% Pits type hypoplasia	7%	6%

Table 6.8 : Relative frequency of enamel hypoplasia recorded per species in terms of defect type.

% total hypoplasia per species in modern data	Goats (N=79)	Sheep (N=66)
%. Line type hypoplasia	39%	67%
% Depression type hypoplasia	32%	18%
% Pits type hypoplasia	29%	13%

Table 6.9 : Relative frequency of enamel hypoplasia recorded per species in terms of defect type in the modern dataset.

6.4.3 Identifying and interpreting seasonality

Key Points

- Defects occur in the cervical portions of the tooth crown in all populations and all three molars.
- The modern material and the Elmenteitan site of Ngmuriak have very similar distributions of enamel hypoplasia on tooth crowns.
- All sites show a peak of enamel hypoplasia at approximately 6 months.
- The sites of Lemek North East and Narosura have similar distributions of enamel hypoplasia on tooth crowns.

General Results

The archaeological material shows very similar distributions on the tooth crown to those identified by Balasse, et al. (in press) shown in Figure 6.9, with the majority of the hypoplasia located in the cervical half of the tooth. Distributions of enamel hypoplasia between sheep and goats were compared between all the archaeological sites but no differences were observed. As there were no metric differences in terms of tooth crown height between sheep and goats there was no need to plot them separately; consequently both species are plotted together (Shown in Figure 6.10 to Figure 6.13). In all of the material on the first molars the majority of the hypoplastic defects occur in the cervical 15mm of the tooth crown. On the second molar the majority of defects occur in the cervical 17 mm of the tooth crown. A similar pattern is found in the third molar, with the majority of defects occurring in the cervical 23 mm of the tooth crown.

In the study by Balasse, et al. (in press) no seasonal trends were identified in the data. However, the data was only analysed using basic histograms and did not explore the data further e.g. using running means or adjusting for variation in development rates down the tooth crown. A re-analysis of the modern material was carried out, calculating running means for the relative frequency values, as discussed in Chapter 4. The results of this analysis on the modern and archaeological assemblages are shown in Figure 6.14 to Figure 6.17, plotted onto the crown development rates for

sheep teeth. Unfortunately, the site of Enkapune Ya Muto produced a data-set that was too small to be included in this analysis.

Peaks of enamel hypoplasia in the modern specimens (Figure 6.14) occur at 6 months after birth on the first molar and around 7 months after birth on the second molar. On the second molar there is a subsequent increase in the occurrence of enamel hypoplasia between 11 and 15 months with a possible slight decrease in the number of enamel hypoplasias around 13 months after birth on the posterior cusp. A small peak of hypoplasia is seen on the third molar at 20 months, with another peak occurring around 26 months after birth. The Elmenteitan site of Ngmuriak (Figure 6.15) is very similar to the modern material in terms of the distribution of enamel hypoplasia, with a single large peak on the first molar occurring between 5 and 6 months. The second molar shows a large peak between 10 and 15 months with a slight decrease in the occurrence of hypoplasia at 12 months. The third molar from Ngmuriak has 2 peaks of hypoplasia, one small, one at 20 months and another at 26 months.

At Lemek North East (Figure 6.16) the distribution of enamel hypoplasia on the first molar is not clear due to small sample size, but there appears to be a peak of hypoplasia located around 3 to 4 months after birth. On the second molar a small peak occurs at 6 months and a large peak at 12 to 14 months. On the third molar a minor peak occurs at 16 to 17 months with large peaks occurring around 22 months and 28 months. Similar distributions are also seen at Narosura (Figure 6.17), with a single large peak occurring on the 1st molar at 3 to 4 months and two peaks on the second molar at 6 months and 11 to 12 months. On the third molar a small peak is located at around 20 months with a large peak at between 26 and 27 months.

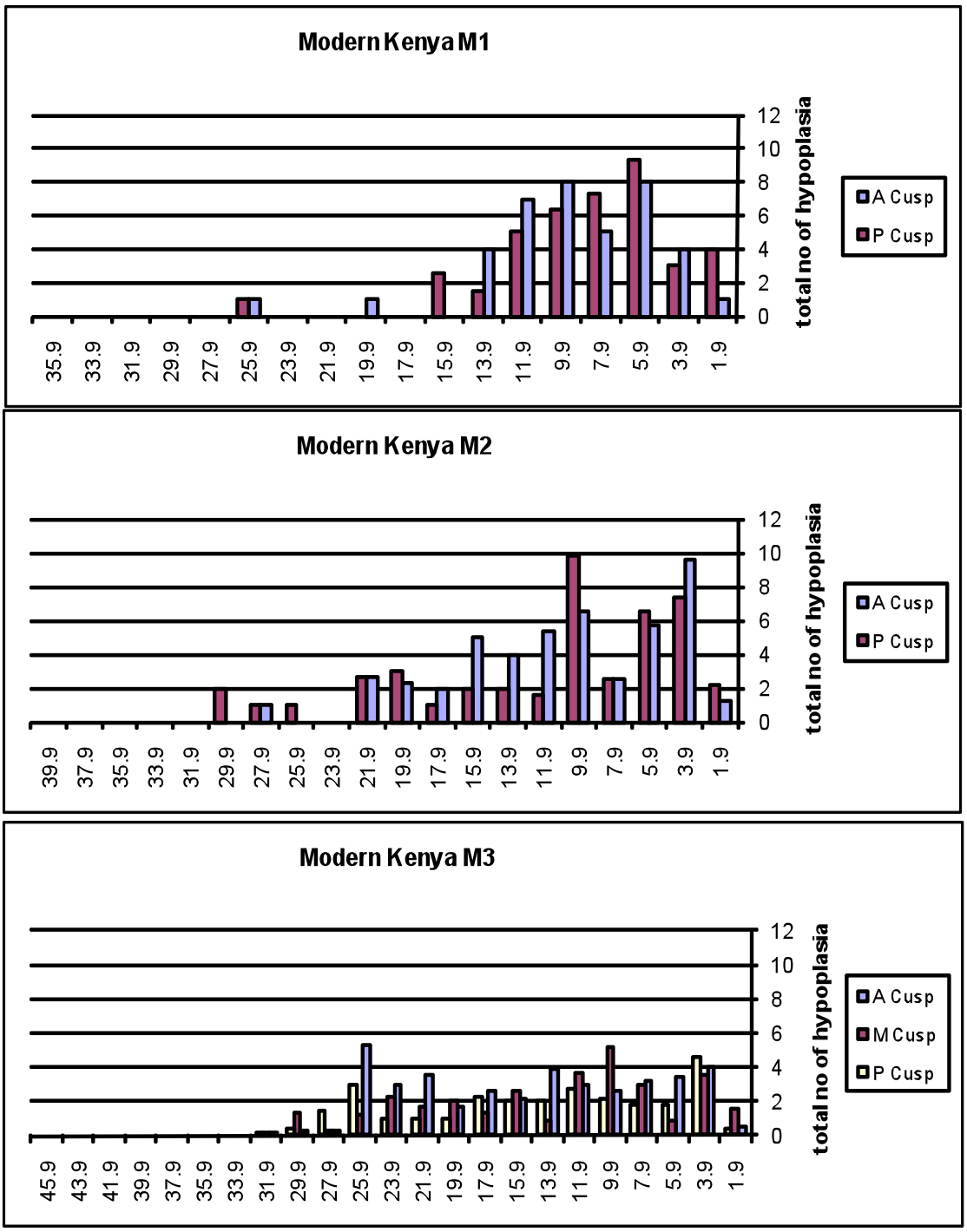

Figure 6.9: The location of hypoplasia on the tooth crown of M1, M2 & M3 in the modern caprine material, plotted in millimetres from the root enamel junction (REJ) on the right of the graph to the maximum height of the tooth cusp (calculated from all available teeth) on the left of the graph. (A=anterior, P=posterior - M=middle cusp of M3).

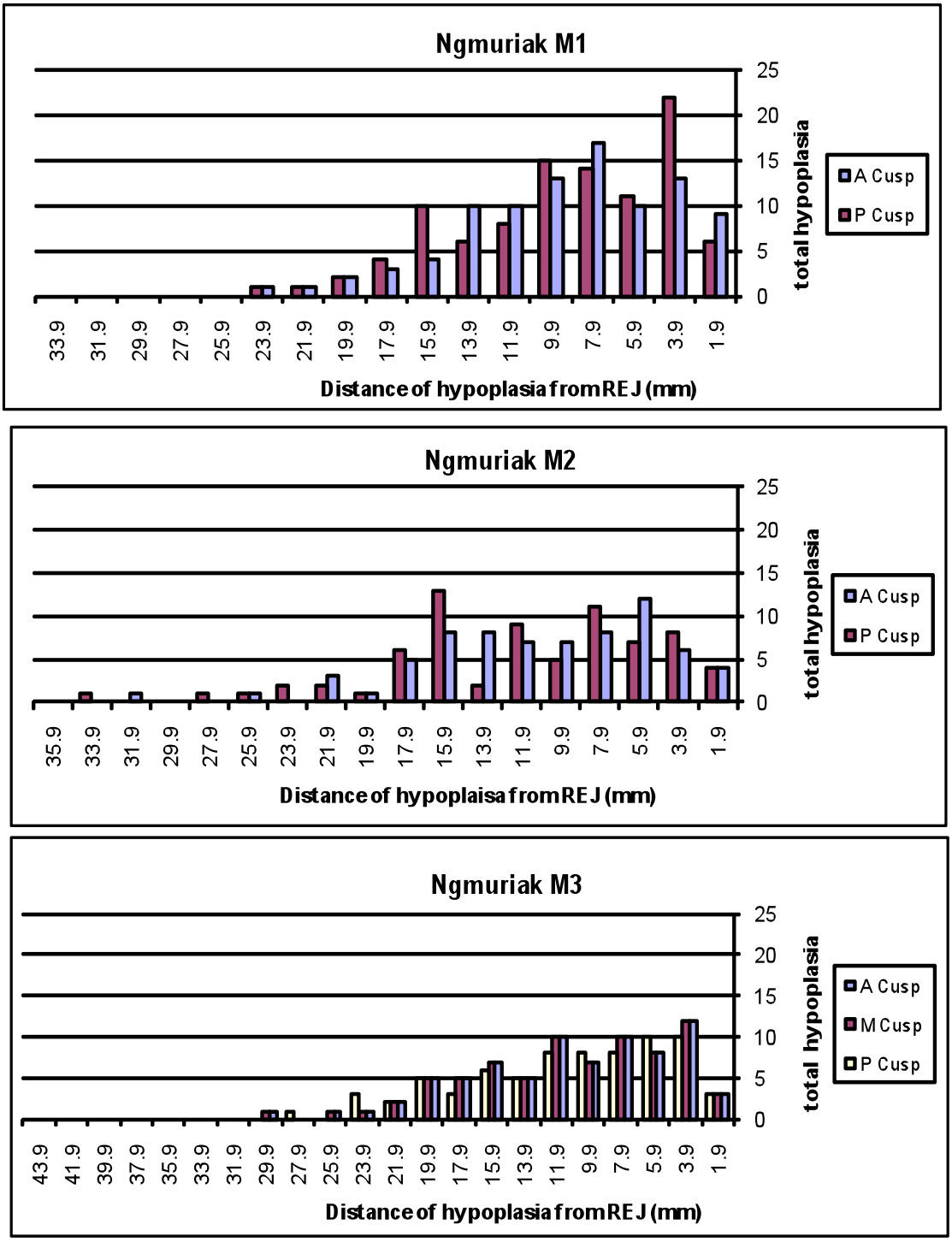

Figure 6.10: The location of hypoplasia on the tooth crown of M1, M2 & M3 in the Ngmuriak caprine material, plotted in millimetres from the root enamel junction (REJ) on the right of the graph to the maximum height of the tooth cusp (calculated from all available teeth) on the left of the graph. (A=anterior, P=posterior - M=middle cusp of M3).

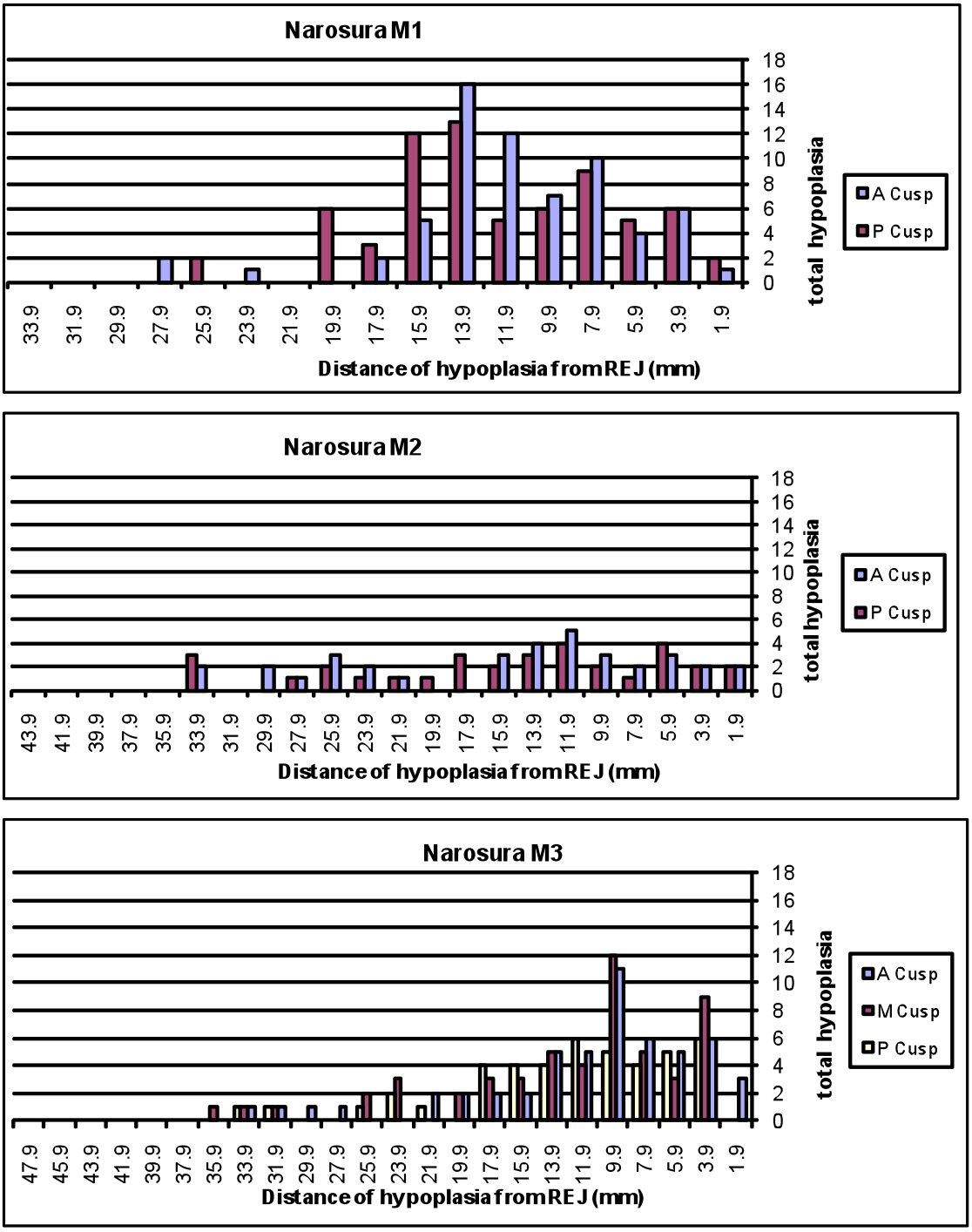

Figure 6.11: The location of hypoplasia on the tooth crown of M1, M2 & M3 in the Narosura caprine material, plotted in millimetres from the root enamel junction (REJ) on the right of the graph to the maximum height of the tooth cusp (calculated from all available teeth) on the left of the graph. (A=anterior, P=posterior - M=middle cusp of M3).

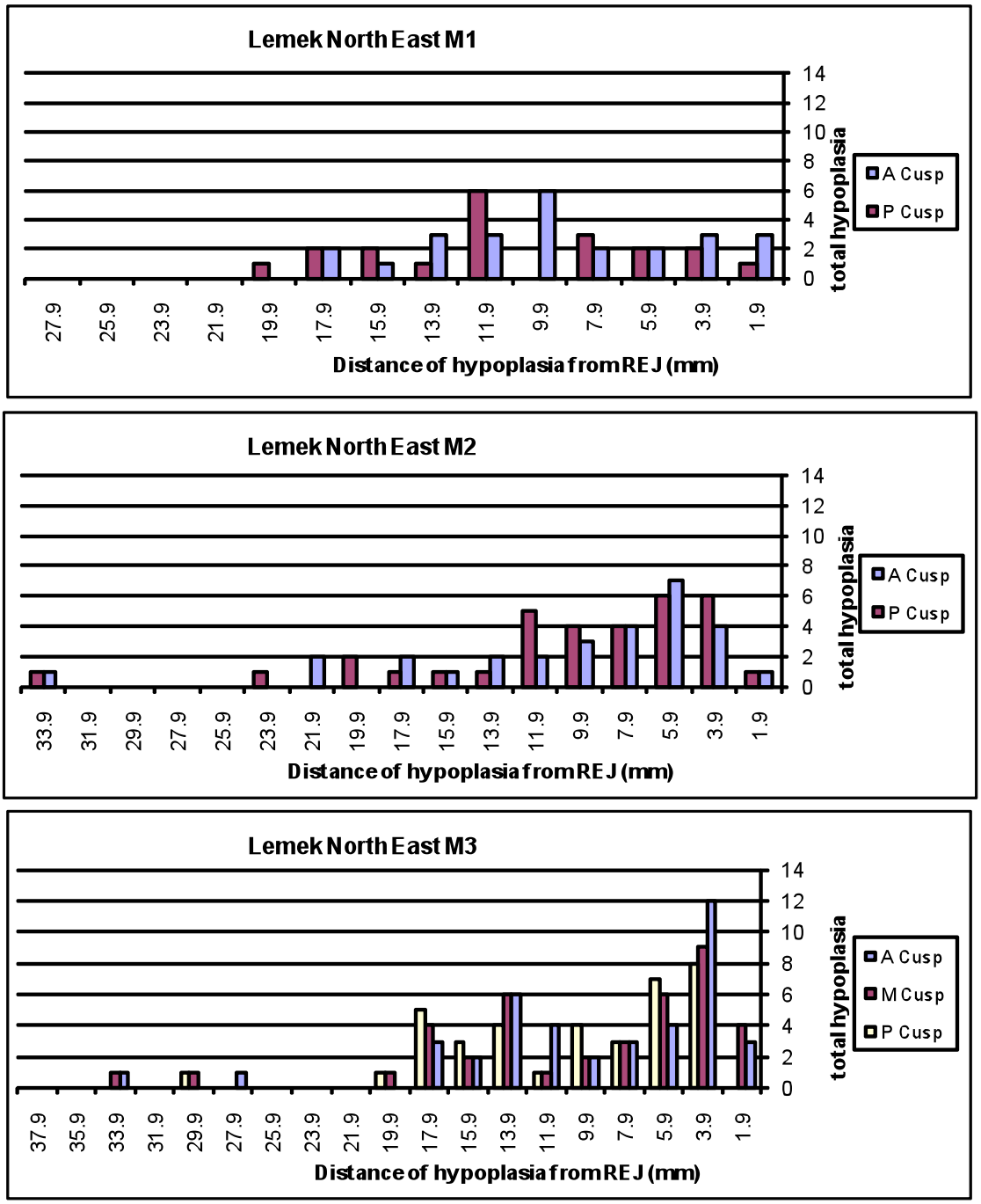

Figure 6.12: The location of hypoplasia on the tooth crown of M1, M2 & M3 in the Lemek North East caprine material, plotted in millimetres from the root enamel junction (REJ) on the right of the graph to the maximum height of the tooth cusp (calculated from all available teeth) on the left of the graph. (A=anterior, P=posterior - M=middle cusp of M3).

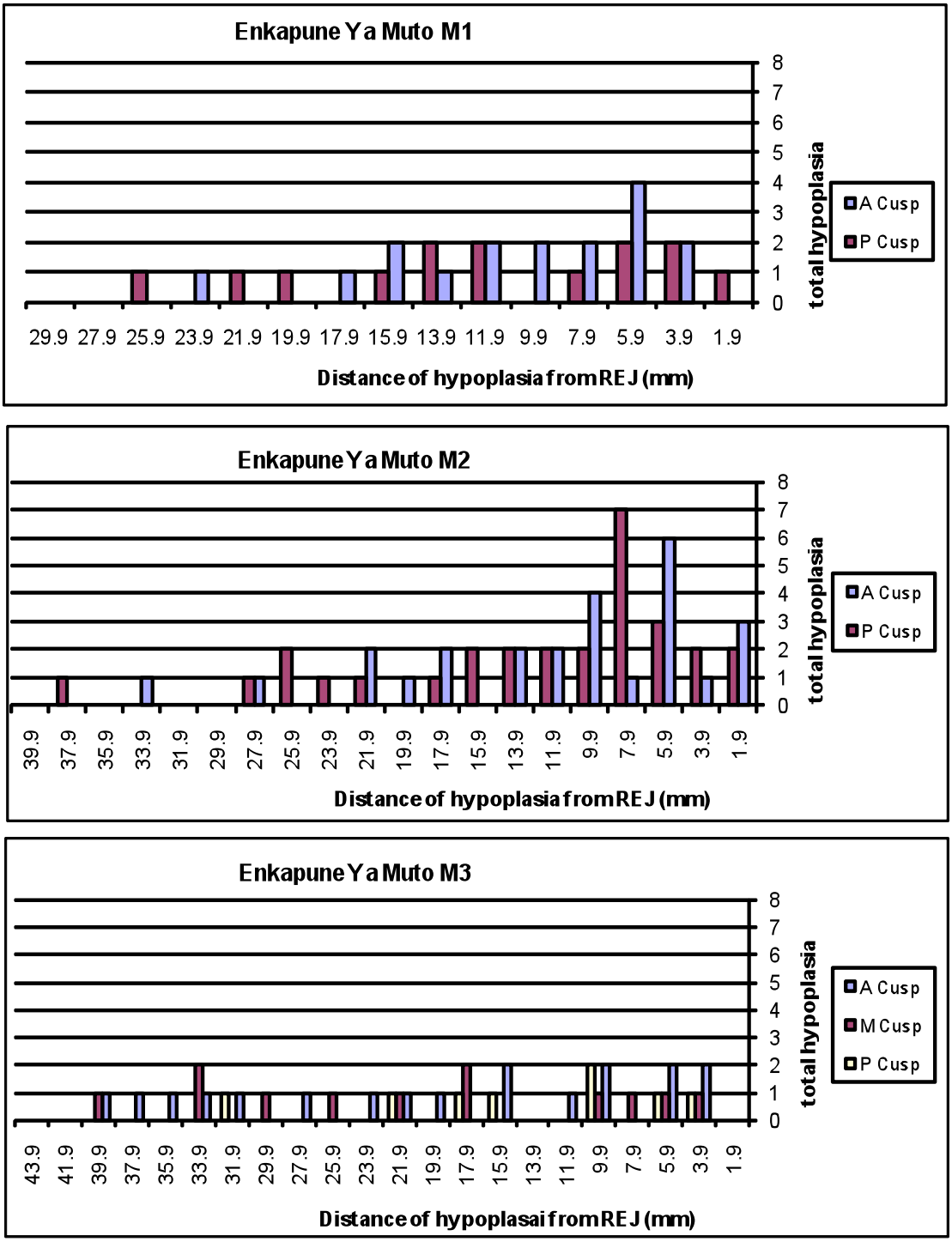

Figure 6.13:The location of hypoplasia on the tooth crown of M1, M2 & M3 in the Enkapune Ya Muto caprine material, plotted in millimetres from the root enamel junction (REJ) on the right of the graph to the maximum height of the tooth cusp (calculated from all available teeth) on the left of the graph. (A=anterior, P=posterior - M=middle cusp of M3).

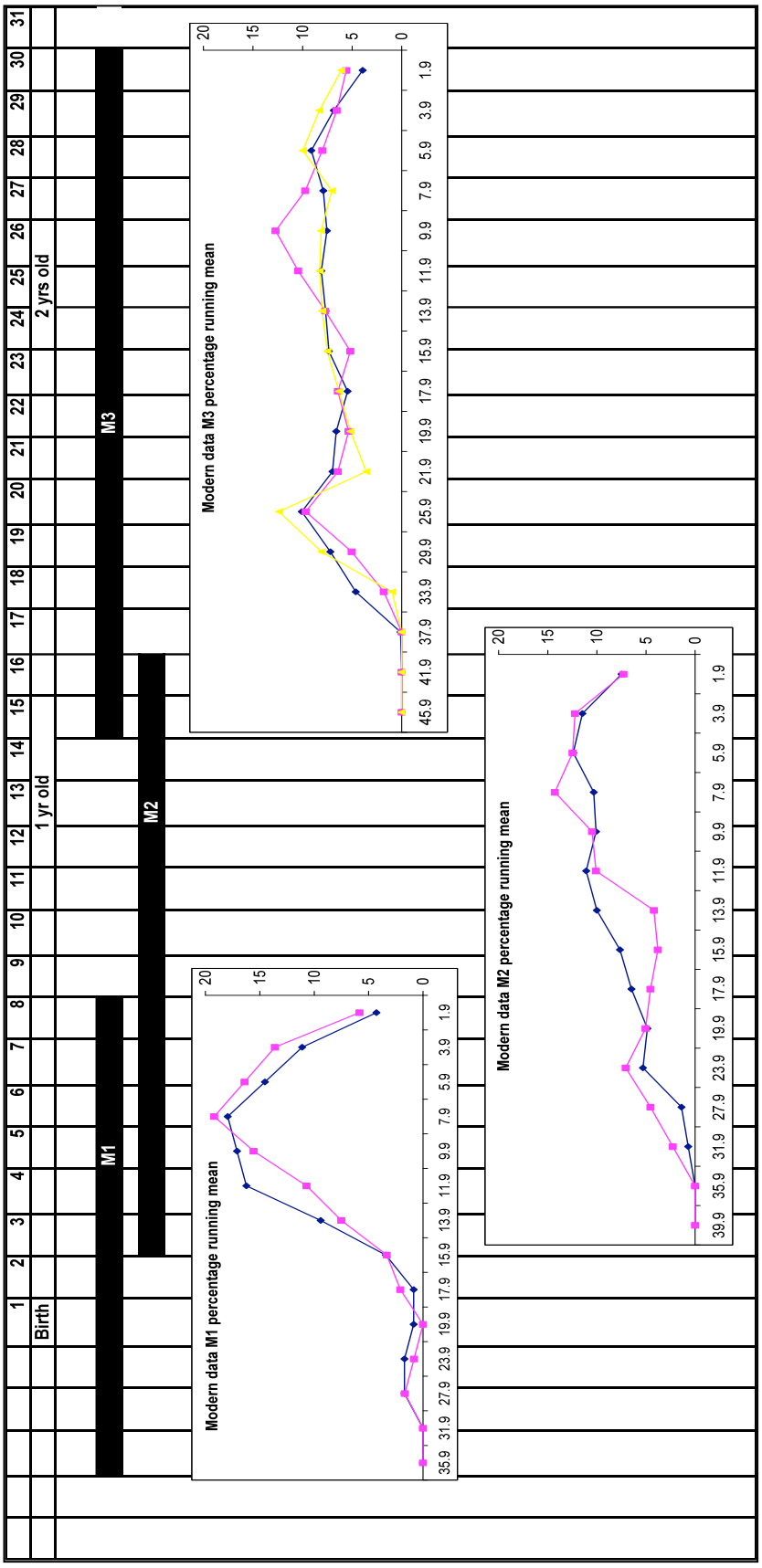

Figure 6.13: The modern material from Kenya plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in millimetres. The Y axis shows the relative frequency of hypoplasia present.

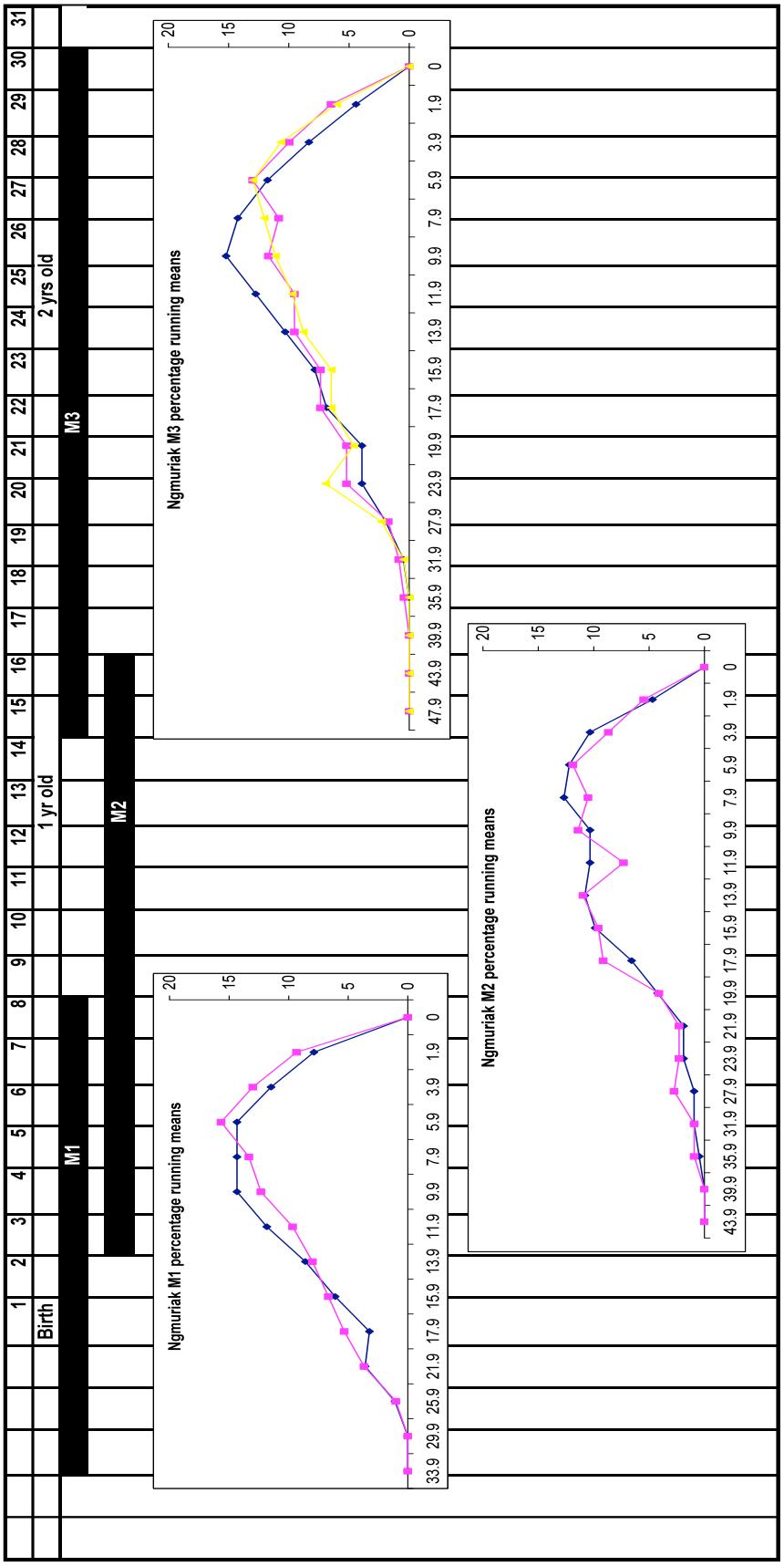

Figure 6.13: The material from Ngmuriak, Kenya plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in millimetres). The Y axis shows the relative frequency of hypoplasia present.

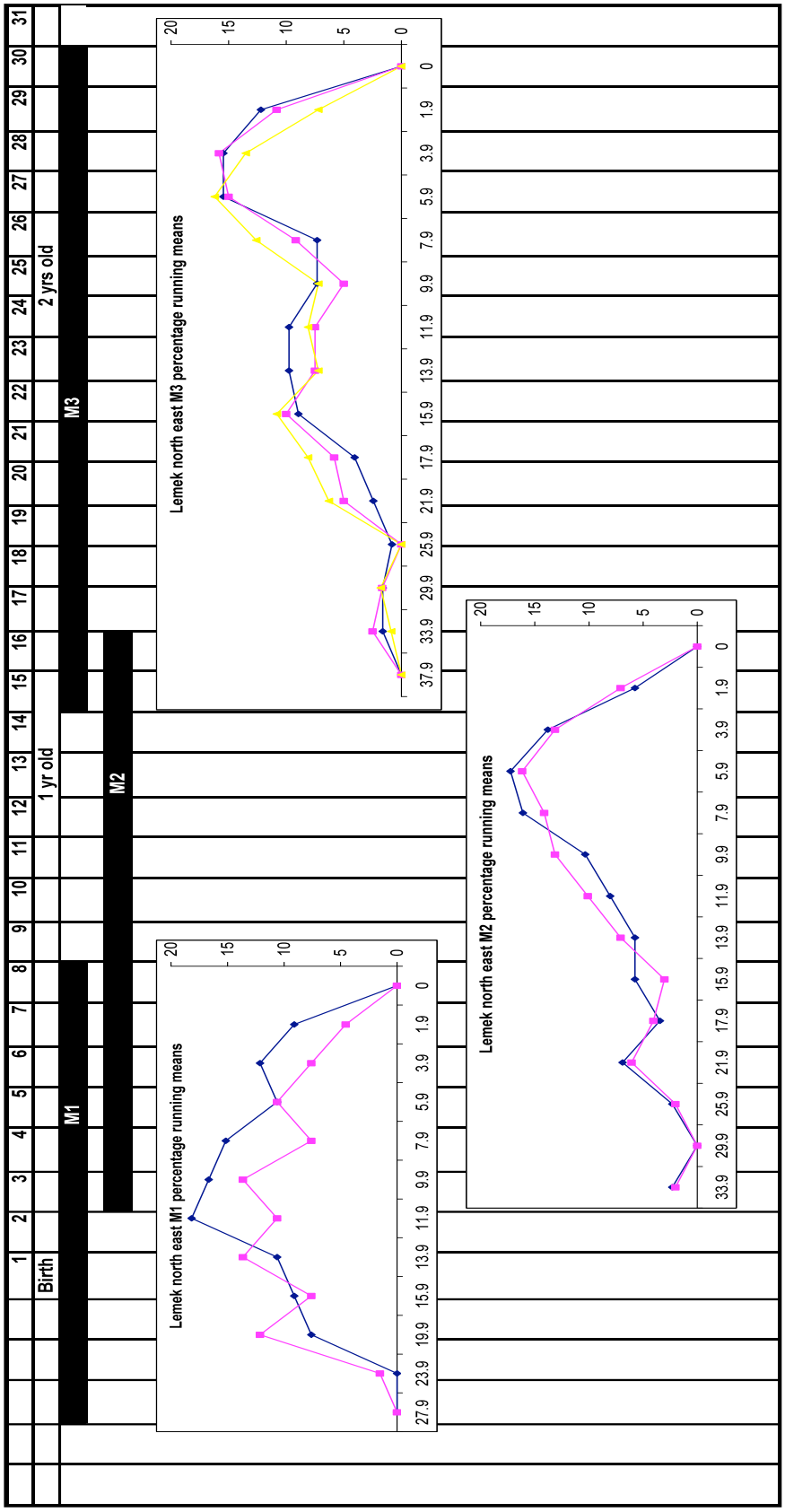

Figure 6.13: The material from Lemek North East, Kenya plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in millimetres). The Y axis shows the relative frequency of hypoplasia present.

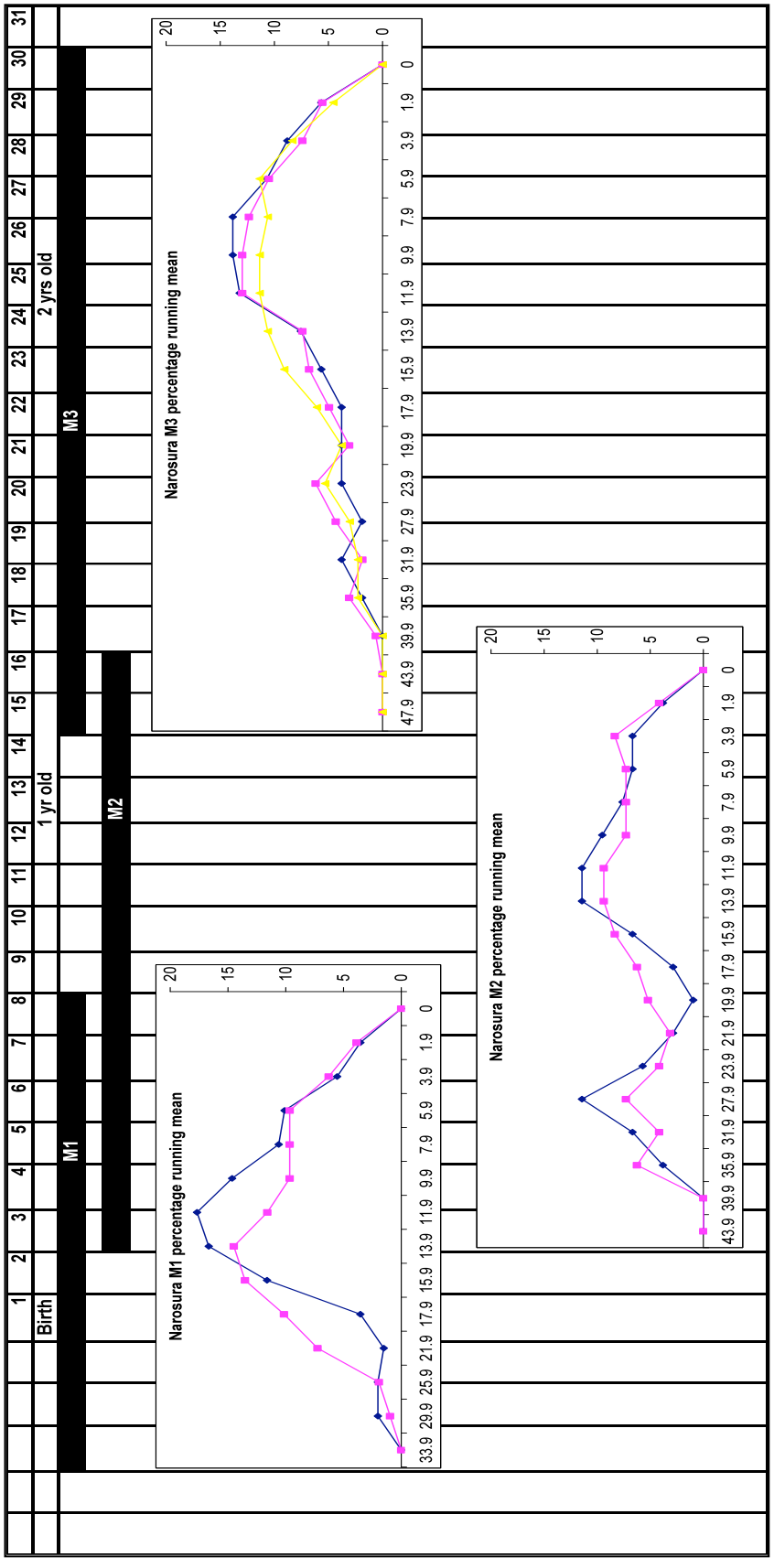

Figure 6.13: The material from Narosura, Kenya plotted as percentage running means onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in millimetres). The Y axis shows the relative frequency of hypoplasia present.

6.5 Discussion

6.5.1 Interpreting animal husbandry practices

The fact that there are no significant differences noted between the separate cultural groups in any of the parameters studied suggests that, in terms of general animal management strategies at least, they may have been broadly similar. This is not surprising, as both cultures practised a specialised form of pastorialism, as discussed previously. The only major differences in patterns of enamel hypoplasia observed were between the different types of sites studied.

The rock shelter site of Enkapune Ya Muto in the Rift Valley stands out from the open plain sites with a considerably higher frequency of enamel hypoplasia than all the others sites studied. This result is surprising as the modern data suggests that caprines from the more mesic habitat of the Rift Valley produce fewer hypoplastic enamel defects than those from the semi-arid region of Narok South - a result of ecological buffering against seasonal droughts (Balasse, et al. in press). Enkapune Ya Muto also stands out from the other archaeological sites, with goats apparently suffering more physiological stress than the sheep at the site (revealed as higher frequencies of hypoplasia and significantly higher levels of more severe hypoplastic defects). Goats from the Enkapune Ya Muto rock-shelter site in the Rift Valley also suffered from considerably more stress than goats from the open plain sites.

It has been suggested by Robertshaw, (1988) that the rock shelter sites may have been used more as seasonal camps than the large open site settlements which served as permanent occupation sites. Robertshaw (1988) and Ambrose (1984) suggest that there may have been a degree of economic differentiation within Elmenteitan society with different settlements having different livestock management patterns. This is supported by the settlements found in the region of the Mau escarpment with high elevation sites consisting of large open area settlements and the low elevation sites

being almost exclusively located in small rock shelters with faunal assemblages that are almost entirely composed of caprine remains (Ambrose 1984). Robertshaw (1988) goes on to suggest that this may be indicative of seasonal herding of goats down to the floor of the Rift Valley.

Isotopic analysis of sheep from the site of Enkapune Ya Muto by Balasse & Ambrose (2005a) suggested that, although some of the sheep were herded all year round down in the valley floor with the cattle, others were also herded at a similar elevation to the settlement itself. The thick layer of burnt dung present within the rock shelter suggests that, in some periods, animal were almost certainly kept penned within the rock shelter and its surrounding area (Ambrose 1998; Balasse & Ambrose, 2005a). It is possible that at Enkapune Ya Muto sheep and goats may have been herded separately, explaining the disparity in the occurrence of enamel hypoplasia between the species at this site. Possibly the majority of the goats were herded with a few sheep in the dryer conditions of the valley floor while the remaining sheep were kept close to the settlement site. Alternatively, similar high levels of stress could have been induced by goats being penned into a confined space in the shelter whilst the sheep were herded around the settlement and down on the valley floor. Obviously a more detailed isotopic analysis of this material is needed to investigate the movements and herding of goats at this site, but the enamel hypoplasia data clearly shows the animals are beginning managed in a different way to the animals from the other archaeological sites studied. While it cannot be said for certain that this is due to sheep and goats being herded separately or to seasonal mobility between the valley floor and the site, this interpretation would appear to fit rather well with the archaeological evidence.

6.5.2 General differences between sheep and goats

The higher number of goats compared to sheep was expected in the archaeological populations since three of the sites are located in the semi-arid region of Narok South and higher numbers of goats are common in modern pastoral groups in this region. Goats are considered to be hardier and more tolerant of the dry conditions and drought periods compared to sheep, which are considered to be picky eaters, requiring more management (Redding, 1981). Enkapune Ya Muto is the only site located in the more mesic region of the Mau escarpment at 2400m, which may explain the higher number of sheep found at this site.

It was expected that there would be a difference in the frequency of enamel hypoplasia between sheep and goats, as found previously by Balasse, et al. (in press), with sheep having higher frequencies of enamel hypoplasia, as well as more severe hypoplasia. Surprisingly however, in this further study of archaeological material from the same region, sheep and goats showed no difference in the frequency of hypoplasia, but overall, sheep did show higher defect severity levels than goats. The fact that no differences were identified between sheep and goats in terms of the distribution of defects on the tooth crown suggests that physiological / environmental factors were affecting both populations equally and at the same times. But the higher severity levels indicate that sheep were perhaps more compromised by them.

Biologists working with both species agree that goats can survive and even thrive in areas that will not support the minimum nutritional requirements for sheep (Williamson & Payne, 1959; Malechek & Leinweber, 1972; Huston 1978). Preferences for browsing by goats and predominant grazing by sheep have been described in various semi-arid and tropical environments and in the study area (Balasse & Ambrose, 2005b). Studies by Cory (1972 cited in Redding, 1981) suggest that goats' diets consist of 38% grazing, 53 % browsing and 9 % from other sources, while sheep are 80% reliant on grazing and just 10 % on browsing, with 10% of their diets coming from other sources. Goats are well known for their ability to consume a

wide range of materials (See Figure 6.14) and browse from a range of low-lying plants such as grasses but also from trees and shrubs, whereas sheep are largely dependant on grassy resources (Redding, 1981).

Figure 6.14: A goat eating a school text book in Egypt! (Upex, 2007)

In times of drought or in poor environments when food is scarce, goats would be able to supplement their diets with a variety of different food sources, whereas sheep would be restricted to low lying grasses and plants. This difference in feeding behaviour implies that sheep would be more severely affected than goats by the rarefaction of grass during drought episodes. It is probable, as discussed by Balasse, et al. (in press), that sheep were slightly more susceptible to dry periods when fodder supplies ran low and that this difference in the underlying nutritional level is responsible for the observed increased severity of hypoplastic defects in sheep teeth.

6.5.3 Identifying and interpreting seasonality : Seasonal physiology and animal husbandry

In the archaeological material detailed here, and the modern data discussed by Balasse, et al. (in press), hypoplastic defects are distributed over the cervical halves of the crowns in all three molars. In the arid and semi-arid zones of Kenya, the reported pre-weaning mortality rate is 10-30% in lambs and 20-30% in kids (Peeler & Wanyangu, 1998), suggesting that the first four months of life of domestic caprines are extremely stressful in these husbandry regimes. However, hypoplastic defects are rare in the parts of the crown representing these chronologic periods in both the archaeological and modern data. This lack of obvious representation of stress in the early developmental periods is not easily explained by dental attrition, as there are still adequate numbers of high crowned and unworn teeth available for study in these populations. As discussed in Chapter 4, it is suggested that the internal structure of the tooth and the different rates of development down the tooth crown are responsible for this apparent reduction in enamel hypoplasia in the occlusal half of the crown. This is supported by the extremely limited numbers of hypoplasia found on teeth with incomplete crowns.

Both birth and weaning are physiological events that cause well documented and visible dental defects (see Chapter 3 for a more detailed discussion). The previous chapter demonstrated that these stressors were visible in the enamel hypoplasia record from caprine populations in Orkney. The question remains whether (as expected) these events can be identified in the caprine material from Kenya, and if they can be used to reveal differences between the sites and their animal husbandry strategies.

<u>Birth</u>

In the modern population and the archaeological population from Narosura (Figure 6.14 to Figure 6.17 above in section 6.4.3), a very small peak of enamel hypoplasia is

identified occurring around the time of birth, although in both populations this peak is not large enough to be statistically valid. None of the other Kenyan populations studied have any peaks of hypoplasia relating to birth. This is not perhaps not surprising as in ungulates birth is normally a quick process, necessitated by the vulnerability of the mother and the young to predation. However, this result is unusual given the clear peaks of enamel hypoplasia associated with birthing stress in material from Orkney (discussed in the previous chapter). It may be that there are additional factors such as climate (e.g. low spring temperatures) impacting on neonatal caprines in the Orkney, which are not present in the Kenyan data.

Weaning

In all populations a large peak of enamel hypoplasia is recorded in the cervical half of the first molar (M1). This peak of enamel hypoplasia must be seen as relating to a stress event occurring after birth but before the animal has reached 8 months of age (when the development of the first molar is completed). It is most probable that weaning and the associated nutritional and physiological stresses that accompany this period are responsible for this peak of hypoplasia.

There is however a slight variation in the timing of this defect between the modern and Ngmuriak (ELM) populations and Lemek North East and Narosura (SPN) populations. In the modern population and the archaeological assemblage from Ngmuriak (Figure 6.14 & Figure 6.15 above in section 6.4.3) a single large peak of enamel hypoplasia occurs on the first molar around 6 months after birth. The second molar (M2) in these two populations also shows a slight peak in the most occlusal half of the crown, again occurring at 6 months after birth. These peaks of enamel hypoplasia in the first and second molar in these two populations (modern and Ngmuriak) are almost certainly related to weaning. It is interesting to note here that while these two peaks clearly overlap (indicating that they are caused by the same events), in both populations the peak of enamel hypoplasia in the second molar is

considerably smaller than that in the first. This is an artefact of the different development rates occurring down the tooth crown, as discussed in Chapter 4.

The timing of weaning in Lemek North East and Narosura (the two SPN sites, shown in Figure 6.16 & Figure 6.17 above in section 6.4.3) is slightly harder to interpret. In both of these populations there is a single large peak of hypoplasia on the first molar, although in the Lemek North East data this is not as clear due to the small sample size. In the modern and Ngmuriak datasets this peak is located in the cervical half of the tooth crown at 6 months after birth however, in both SPN datasets, this peak is located much more centrally at 3 to 4 months after birth. This may suggest that weaning was occurring earlier in Lemek North East and Narosura (SPN) populations than the Ngmuriak (ELM) and modern populations.

From the data collected in the field, it is known that weaning is allowed to occur naturally in the modern population, and the similarity between the modern and Ngmuriak data-sets suggests that this has also been the case at the Elmenteitan site. If weaning is responsible for the peak of enamel hypoplasia on the first molar in the two Savannah Pastoral Neolithic populations, then it raises the possibility that forced weaning was taking place in these populations, by deliberately separating the young from their mothers at an early age (approximately 3 to 4 months after birth according to the location of the enamel hypoplasia peak). Alternatively, this peak may be related to stress caused by birth and the period of malnutrition immediately following birth. This suggests that the Savannah Pastoral Neolithic caprine populations may have suffered greater environmental / physical stress in the months following birth than the modern and Ngmuriak (ELM) populations. This interpretation would make more sense, in terms of agricultural management, as enforced weaning is rarely practised in traditional agricultural systems as it places considerable stress (both physical and mental) on the young (Murphy & Ruiz-Miranda, 1998). It is more commonly found in intensive modern husbandry regimes in industrialised countries, where the diet of the young can be monitored and their diets supplemented as necessary (Murphy & Ruiz-Miranda, 1998). Also, in practical terms, if the

archaeological flocks were managed in a similar way to the modern animals, maintaining the separation of young from their mothers could be difficult as the flocks are allowed to graze freely.

On the second molars in both SNP populations (Lemek North East and Narosura, Figure 6.16 & Figure 6.17 above in section 6.4.3) there are two clearly defined peaks of enamel hypoplasia. The first peak on the second molar occurs, in all the populations studied, between 6 and 7 months after birth. In the modern and Ngmuriak (ELM) data-sets (Figure 6.14 & Figure 6.15 above in section 6.4.3) this peak was explained as weaning due to the clear overlap with the suggested weaning-related peak on the first molar. In the SPN data there is no overlap with a peak on the first molar. However, if the peak on the first molar in the SPN populations is seen as representing a stressful period immediately following birth and not as representing an earlier weaning period, then this first peak on the second molar can be regarded as representing weaning, occurring in all populations studied between 6 and 7 months after birth. This fits with the general assumption that in naturally weaned flocks, complete separation between the mother and the lamb will have occurred by 8 months (Squire, 1975). Consequently, in the preceding months the lamb will have been slowly forced to become increasingly dependant on the surrounding food sources. This peak of enamel hypoplasia occurring at 6 – 7 months may well represent the early stages of this transfer, as the young are getting used to new food sources and learning to forage for themselves (Squire, 1975).

Gestation / lactation and other physiological stressors

In modern Red Maasai sheep, females can reproduce from the age of 12 months onwards (Odenya, 1994). This may suggest that the extended peaks of hypoplasia seen in the cervical half of the second molar in all populations maybe related to animals undergoing their first gestation. However, if this were the case, then it would be expected that the peak of stress would continue for the whole 5 months of gestation, which it does not. It would also be expected (allowing for five months of

gestation) that around 17 and 18 months the physical stress of birth and lactation would be visible as peaks of hypoplasia, but in all populations there are no peaks located around this period.

Other possible explanations for the peaks of enamel hypoplasia in the second and third molars included seasonal cycles of parasitic or infectious disease leading to an increase in the occurrence of physical stress. The Red Maasai sheep breed, which are the predominant breed in the modern sample, have a high genetic resistance to many types of internal parasites, suggesting that infectious diseases are a more likely cause (Baker, et al. 2002). Another explanation may relate to the intra / inter family alliances that are known to exist in the modern populations. These alliances allow animals to be moved over long distances in search of viable water sources in seasonal periods of drought and it may be that stress caused by this seasonal mobility is also partly responsible for the peaks of hypoplasia.

6.5.4 Identifying and interpreting seasonality: Climatic seasonality

If some of the stress episodes are linked to the seasonal deterioration of environmental conditions, then a distribution of hypoplastic defects mimicking that of the seasonal cycle could be expected. However, in order for seasonal patterning to be identified in the enamel hypoplasia distribution on the tooth crown, there needs to be a clearly defined season of birth, to ensure that seasonal events affect all animals when they are at a similar age. In Kenya, however, this is not the case, since animals can be born at any point throughout the year. However, it will be argued here that there are potentially two main recognisable periods of birth in Kenya linked to seasonal rainfall patterns.

<u>The modern climate in Kenya and its impact on birthing seasons</u>

As discussed above, Kenya's location within the Inter-Tropical Convergence Zone means it has a unique bimodal rainfall pattern (Davies, et al. 1985). This pattern

hypothetically allows animals to be born in two principal annual cohorts. In modern cattle pastoral systems in Kenya there is a clear relationship between the bimodal rainfall and the productivity of the herds, related to the level of milk production (Dahl & Hjort, 1976; Western & Finch, 1986). Rainfall has an effect on the fecundity of the cattle, with animals often failing to conceive or come into season in the dry months, consequently there are strong seasonal patterns in cattle births in areas with just one rainy season and this can lead to milk shortages in the intervening periods Lactation is also very easily affected by the amount of fodder available (Dahl & Hjort, 1976; Western & Finch, 1986). In dry periods there is a tendency for lactation to cease after only a few months because of fodder shortages and the milk produced in these periods can contain half the amount of fat compared to milk produced in the wet seasons (Western & Finch, 1986). The bimodal rainfall pattern in East Africa significantly increases the potential for milk production from pastoral herds and allows a greater reliance on specialised pastoral subsistence patterns. The development of this rainfall pattern is hypothesised to be one of the major reason for the adoption of the highly specialised pastoralist lifestyle which first developed over 3,000 years ago and is still seen in Kenya today (Marshall, 1990b).

As with cattle, caprine fertility levels are also controlled by the amount of fodder available; animals will often only conceive if fat and nutrition levels are normal. Studies from primitive breeds of sheep such as the Awassi, support this, suggesting that animals will often only conceive once the grazing has improved and animals have recovered from the drought periods (Barr, 1968). In terms of animal management strategies for areas with bimodal rainfall patterns, this also makes good sense, as animals will conceive at the end of one rainy season and, allowing for a five month gestation period as commonly found in primitive sheep breeds, the young will then be born at the beginning of the following rainy season (Odenya, 1994). This means that there will be adequate fodder available for the females, allowing them to produce enough milk to sustain the young.

Palaeoclimatic reconstruction in Kenya

Over the last 12,000 years there has been a considerable degree of variation in the climate, and subsequently the vegetation in eastern Africa. Well documented pollen cores from Pilkington Bay in Lake Victoria have demonstrated that the African climate has changed considerably in the last 14,000 years (Stager, et al. 1997). Four distinct climatic phases have been identified: a dry period from between 11,400 to 10,000 BP; a humid wet period between 10,000 and 7,200 BP; a period of increasing seasonality between 7,200 and 2,200 BP and a period of increasing aridity between 2,200 and 0 yrs BP (Stager, et al. 1997). This suggestion of increasing seasonality between 7,200 and 2,200 is also supported by pollen analysis from Lake Victoria by Stager & Mayewski (1997) who suggest that there was an abrupt change in climate in Africa around 7800 BP leading to increased rainfall seasonality. Inferred aridity from the pollen evidence also increases after 7,200 BP (Stager & Mayswski, 1997) supporting earlier evidence suggesting that the climate between 5,600 and 3,000 BP was generally warmer and drier than in the present (Hamilton, 1982; Livingstone, 1975, 1980).

This climatic reorganisation occurring between 6,000 and 3,000 BP is widely recognised across the whole of tropical Africa (Nicholson & Flohn, 1980). It is suggested that this is related to a pole-ward extension of the Inter-Tropical Convergence Zone altering the pattern of the rainy seasons (Nicholson & Flohn, 1980, Partridge, 1993). This ties in with evidence from Lake Naivasha where sediment cores indicate that there was a single rainy season occurring in this region between approximately 9,200 and 2,500 BP, suggested by a light and a dark sediment lamination occurring within one radiocarbon year (Richardson & Richardson 1972). Nicholson and Flohn (1980) suggest that before this period of reorganisation there was an increase in the thermal contrast between the northern and southern hemispheres, causing the Inter-Tropical Convergence Zone to be placed further to the north, leading to a single rainy season in East Africa.

Clearly there is difficulty interpreting this climatic data. Many papers (e.g. Bergner & Trauth, 2003; Bergner, et al. 2004) in their study of lake levels in the last 175,000 years, and Taylor et. al., 2005 in their investigation of vegetation dynamics of the region in the mid to late Holocene) just assume that the bimodal rainfall pattern is in place for the period under investigation. Papers which do discuss the climatic change occurring in this period often suggest varying dates for these changes, making interpretation of the climate during 2,000 -3,000 BP (the period of the archaeological sites) very difficult. The only clear evidence for a single rainy season in the region comes from Richardson & Richardson (1972) in their study of the sediment layers from Lake Naivasha. However, their suggestion that a bimodal rainfall pattern is in place by around 2,500 is supported by the evidence suggesting a wide climatic reorganisation occurring in this period. Although the dates are varied, it is suggested that between 7,000 and 2000 years BP the climate in this region becomes increasing drier and more seasonal. This fits with the interpretation that the movement of the Inter-tropical Convergence Zone caused the climate to change in Africa in this period. Marshall (1990b) suggests that the development of the bimodal rainfall pattern is responsible for the specialised agricultural patterns which appear in Kenya around this time. While it cannot be proven that this is the rainfall pattern that was occurring in the period encompassing the archaeological sites included in this study, it is assumed for the purpose of this analysis that it most likely was, and that therefore yearly rainfall patterns were not markedly different from today's (Richardson & Richardson, 1972).

Climatic seasonality in the modern and archaeological material

Based on the discussion of the bimodal rainfall pattern in Kenya it is hypothesized that there is the potential for two main periods of birth to occur in Kenya. The first follows conception at the end of the first rainy season in June, leading to births at the beginning of the following rainy season in November. The second follows conception at the end of the second rainy season in December, leading to births in May, near the end of the first rainy season. When the hypoplasia distributions on the

tooth crown are adjusted, as discussed in Chapter 4, to allow for varying rates of dental development and plotted onto a bimodal seasonal cycle as discussed above, there does appear to be some bimodal distribution in the occurrence of hypoplasia relating to the hypothesized periods of drought: occurring at 8 to 11 months; 14 to 17 months; 20 to 23 months; and 26 to 29 months after birth (see Figure 6.19 to Figure 6.22). Drought causes many potential stresses, but in particular lack of available food leading to malnutrition and heat stress.

Modern climatic seasonality

On the modern caprine material (shown in Figure 6.19), the enamel hypoplasia peaks on the first molar are explained by birth and weaning. On the second molar there is a bimodal distribution (and potentially even a tri-modal distribution of enamel hypoplasia) with a small peak occurring quite high on the tooth crown and then a much larger peak in the lower half, potentially divided in to two sub-peaks - particularly clear in the distribution on the posterior cusp (see Figure 6.19). The first small peak of enamel hypoplasia on the second molar is explained by weaning, if the second peak on the second molar is split into two separate peaks as suggested by the distribution on the posterior cusp, then these two peaks could be linked to the two dry periods occurring between 8 and 11 months and 14 and 17 months. However, it is difficult to ascertain if this second peak is really divided into two sub-peaks, or if this is just an artefact of the data. In terms of the raw counts of enamel hypoplasia in the modern material (shown in Figure 6.9 in section 6.4.3 above) there does appear to be a significant difference in distribution of enamel defects, with a total of fifteen defects found between 2 and 3.9 mm from the REJ, five defects found between 6 and 7.9 mm from the REJ and sixteen defects found between 8 and 9.9mm from the REJ. The distribution of hypoplasia on the third molar in the modern material (Figure 6.19) appears to fit more closely with the seasonal drought periods that are definitely occurring in the modern Kenyan climate, with peaks of enamel hypoplasia occurring between 19 and 20 months at the beginning of the dry season and at 26 to 27 months in the middle of the dry season.

Archaeological climatic seasonality

In terms of enamel hypoplasia distribution in the archaeological assemblages, the Elmenteitan site of Ngmuriak (Figure 6.20) is very similar to the modern material, particularly for the third molar. The second molar from Ngmuriak shows a large peak of enamel hypoplasia in the cervical half of the crown between 9 and 15 months. This large peak is split possibly into two minor peaks at 10 months and 14 months and, as with the modern material these potentially relate to the two dry seasons that at suggested to be occurring between 8 and 10/11 months and 14 and 16/17 months.

The two SPN sites (Lemek North East and Narosura shown in Figure 6.21 & Figure 6.22) have a slightly different distribution patterns to the modern and Ngmuriak material. In the Lemek North East data (Figure 6.21) there is a large peak of enamel hypoplasia on the second molar occurring between the end of the rains and the beginning of the dry season at around 13 months after birth. In the Narosura data-set (Figure 6.22) there is also a large peak of hypoplasia overlapping with a dry to rainy period around 11 months after birth, and there is a possible third peak at around 15 months after birth in the middle of the dry season. Whilst the peaks of enamel hypoplasia in these two populations do not exactly match the hypothesized dry seasons, they are still very close, with only limited overlap occurring with the rainy seasons. This suggests that they could be related to periods of physiological stress brought about by the dry seasons occurring between: 8 and 10/11 months, 14 and 16/17 months and 20 and 22/23 months.

The third molar in all populations (both modern and archaeological) provides the best evidence to support the suggested bimodal drought scenario. In all populations there are two well-defined hypoplasia peaks on the third molars, falling within in the purported dry seasons occurring between 20 and 22/23 months after birth and 26 to 28/29 months after birth. These clear peaks occur in all the populations studied from Kenya and appear to support the assumptions made about the two periods of birth, as well as the assumptions about periods of drought causing increases in the occurrence of hypoplastic enamel defects.

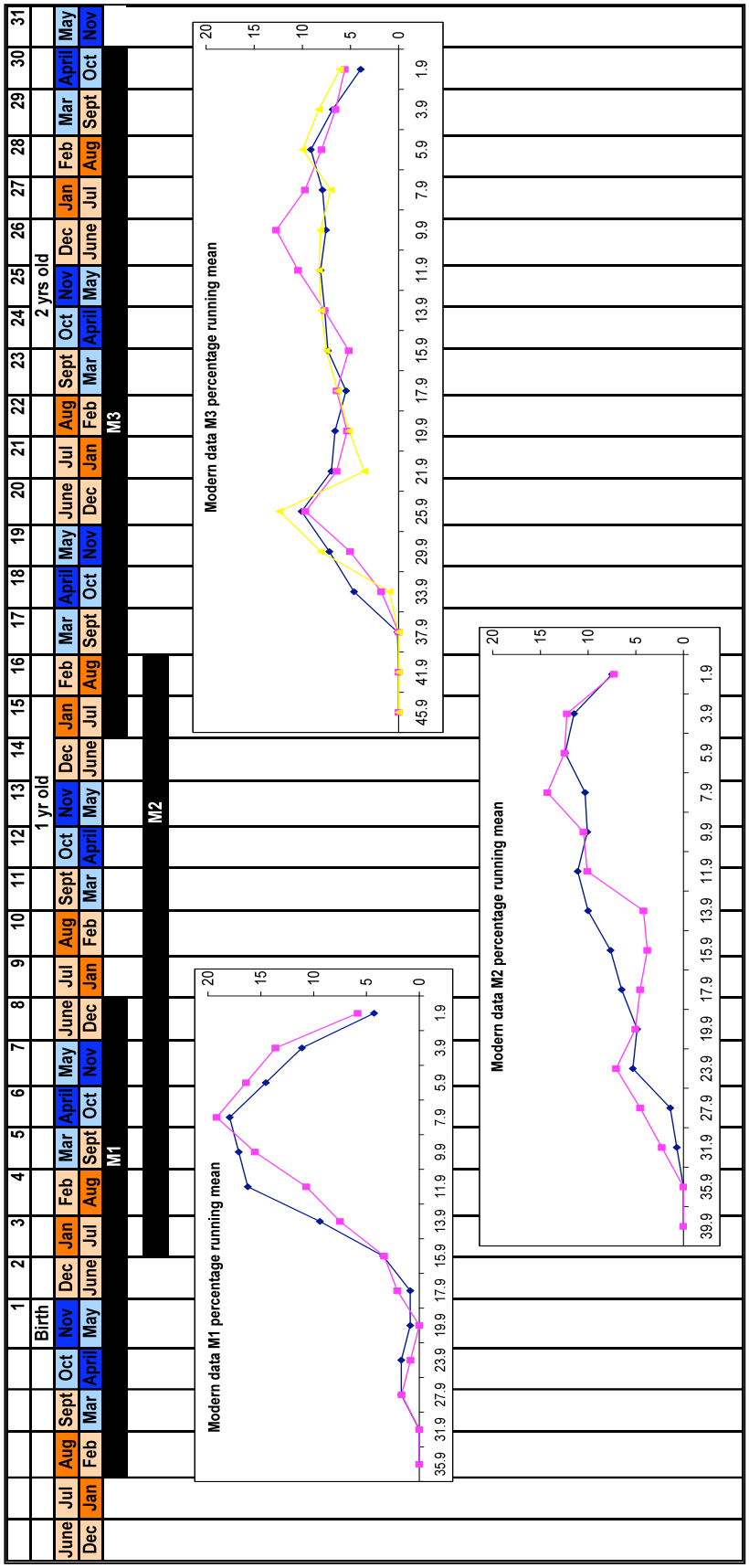

Figure 6.14: Showing the adjusted hypoplasia distribution for the modern material, plotted onto a seasonal calendar, allowing for two seasons of birth. Pink lines = anterior cusp, blue lines = posterior cusp (middle cusp on the third molar) and yellow = posterior cusp on the third molar. Dry and wet seasons shown along the top of the graph with the top line representing conception at the end of the 1st rainy season (birth in November) and the second line representing conception at the end of the 2nd rainy season (birth in May). Blue months = rainy seasons with dark blue showing the wettest seasons, orange/pink months represent the dry seasons with deep orange representing the driest months. Scale along the X axis represents the distance of the hypoplasia from the REJ in millimetres. The Y axis is the relative frequency of hypoplasia.

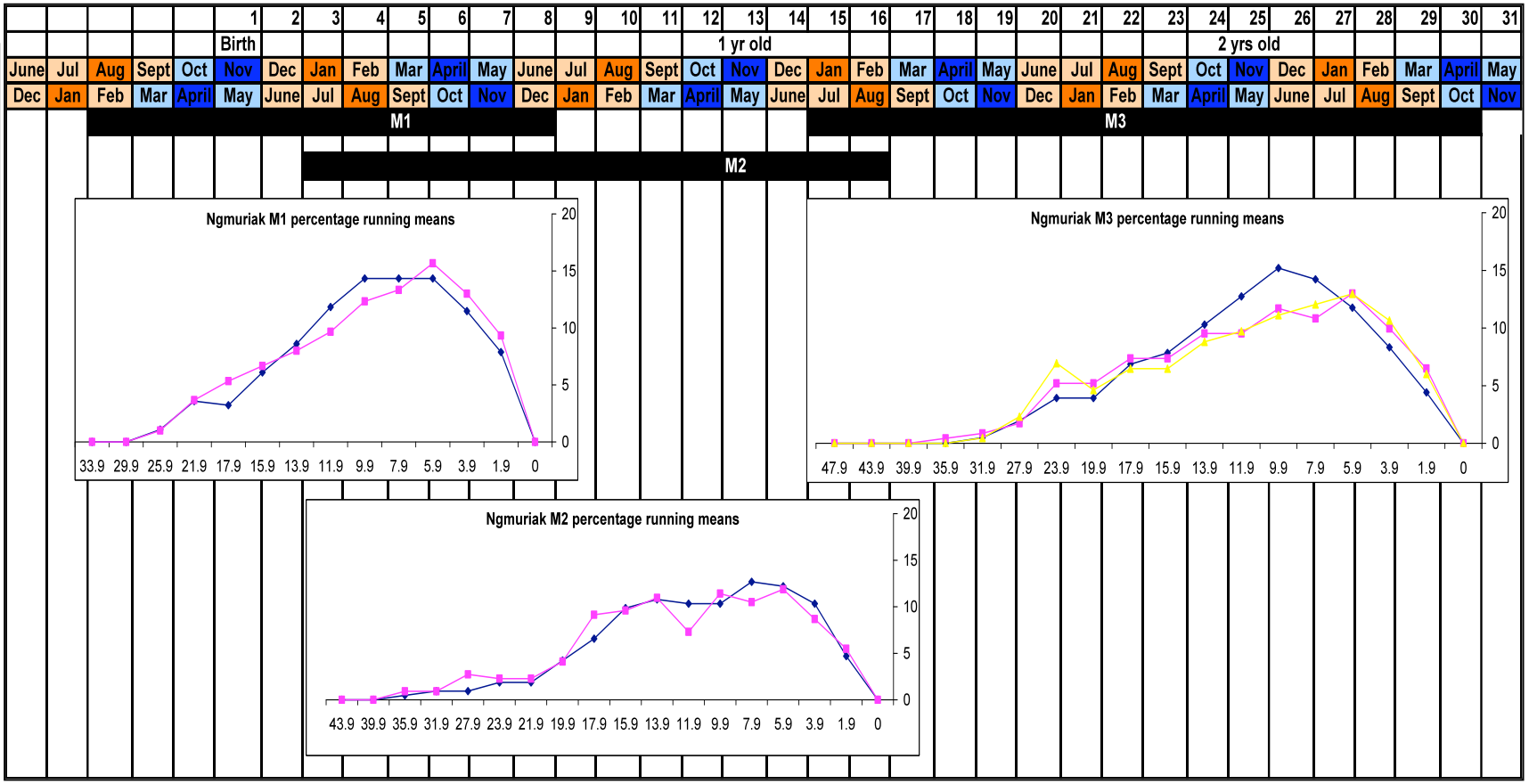

Figure 6.14: Showing the adjusted hypoplasia distribution for Ngmuriak, plotted onto a seasonal calendar, allowing for two seasons of birth. Pink lines = anterior cusp, blue lines = posterior cusp (middle cusp on the third molar) and yellow = posterior cusp on the third molar. Dry and wet seasons shown along the top of the graph with the top line representing conception at the end of the 1st rainy season (birth in November) and the second line representing conception at the end of the 2nd rainy season (birth in May). Blue months = rainy seasons with dark blue showing the wettest seasons, orange/pink months represent the dry seasons with deep orange representing the driest months. Scale along the X axis represents the distance of the hypoplasia from the REJ in millimetres. The Y axis is the relative frequency of hypoplasia.

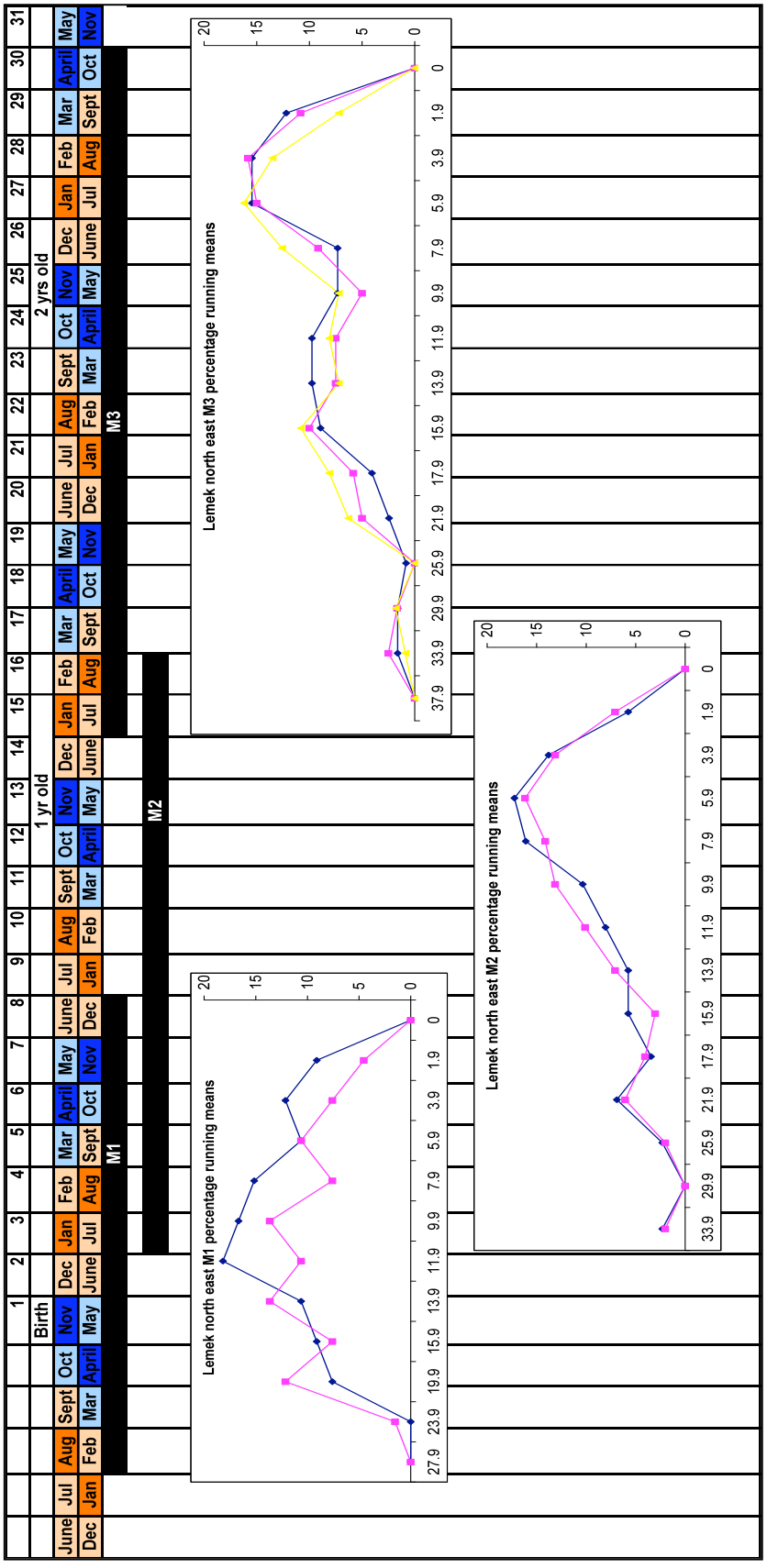

Figure 6.14: Showing the adjusted hypoplasia distribution for Lemek North East, plotted onto a seasonal calendar, allowing for two seasons of birth. Pink lines = anterior cusp, blue lines = posterior cusp (middle cusp on the third molar) and yellow = posterior cusp on the third molar. Dry and wet seasons shown along the top of the graph with the top line representing conception at the end of the 1st rainy season(birth in November) and the second line representing conception at the end of the 2nd rainy season (birth in May). Blue months = rainy seasons with dark blue showing the wettest seasons, orange/pink months represent the dry seasons with deep orange representing the driest months. Scale along the X axis represents the distance of the hypoplasia from the REJ in millimetres. The Y axis is the relative frequency of hypoplasia.

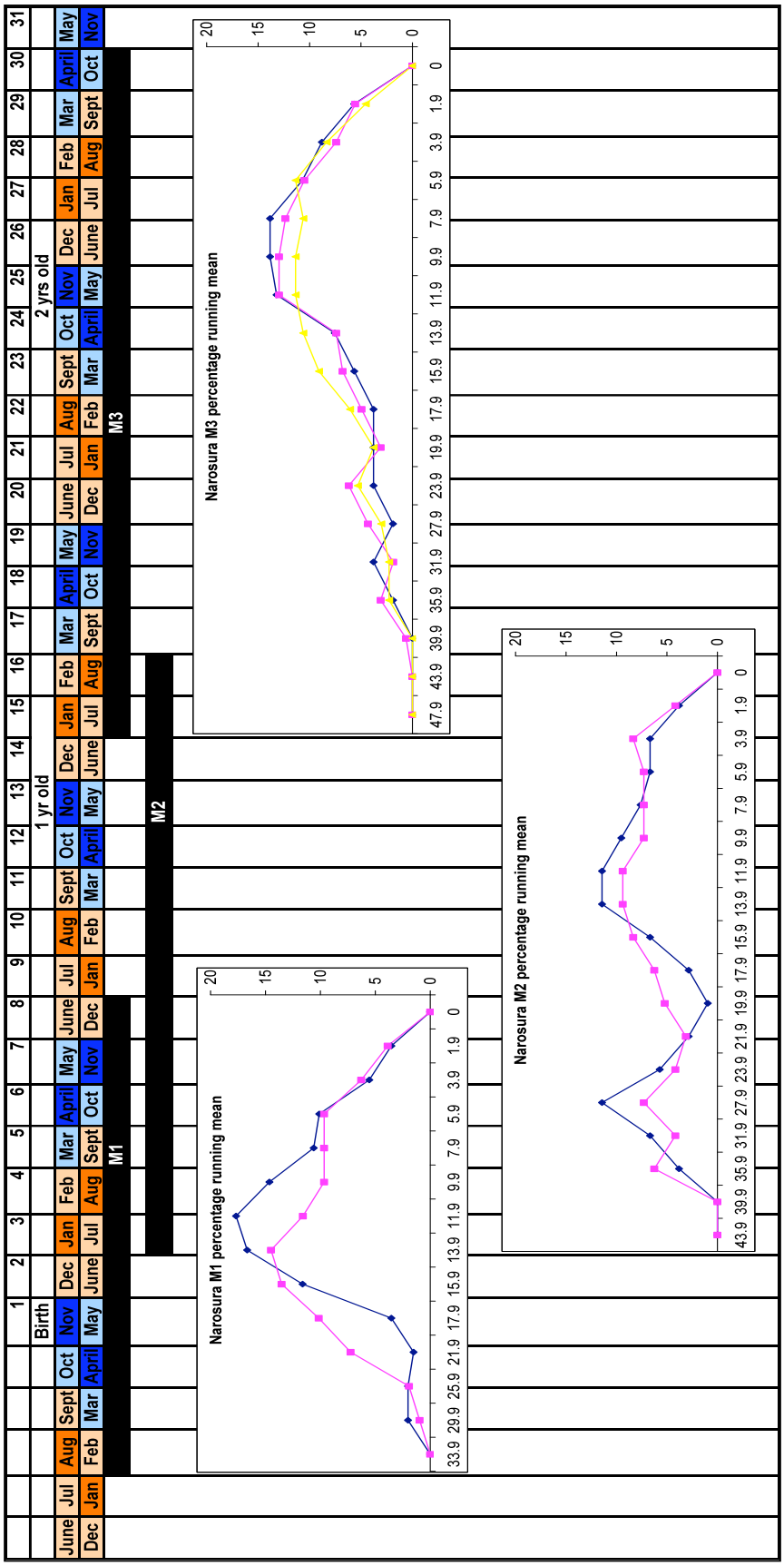

Figure 6.14: Showing the adjusted hypoplasia distribution for Narosura, plotted onto a seasonal calendar, allowing for two seasons of birth. Pink lines = anterior cusp, blue lines = posterior cusp (middle cusp on the third molar) and yellow = posterior cusp on the third molar. Dry and wet seasons shown along the top of the graph with the top line representing conception at the end of the 1st rainy season (birth in November) and the second line representing conception at the end of the 2nd rainy season (birth in May). Blue months = rainy seasons with dark blue showing the wettest seasons, orange/pink months represent the dry seasons with deep orange representing the driest months. Scale along the X axis represents the distance of the hypoplasia from the REJ in millimetres. The Y axis is the relative frequency of hypoplasia.

There are clearly some problems in interpreting these data. The interpretation of the climatic evidence for the archaeological material is difficult, especially with regard to the exact dating of climatic changes occurring in this region. However, as discussed above, it is assumed from the available data that the bimodal rainfall pattern was in place during the periods the archaeological caprine data covers. The fact that the peaks of enamel hypoplasia (especially on the second molar) do not exactly match up with the periods of drought discussed above is also problematic. There are several possible interpretations for this lack of correspondence between the purported dry seasons and the hypoplasia peaks: It is probable that the modern Kenyan sheep have slightly different growth rates than those of the Hoy sheep which were used in the creation of the dental development rate model (see Chapter 4), potentially causing a misalignment between the peaks of hypoplasia and their seasonal causes. There is also no evidence to indicate that the animals studied in Kenya were born in the periods suggested, and even if the majority of animals were born in either of the suggested seasons, then there will almost certainly still be a good number born outside of these two seasons. However, the fact that there are peaks occurring in the data in broadly the right place, does suggest a degree of seasonality in these populations; otherwise peaks would not be visible in the data at all, as discussed by Balasse, et al. (in press) see Appendix 1.

Other causes of hypoplasia are numerous and also have to be considered as possible causes for the peaks observed in the different caprine samples. Infections and parasitic diseases are common in sheep, and infectious conditions are reported as common causes of death in modern Kenyan populations (Peeler & Wanyangu, 1998). If the peaks of hypoplasia are not related to the purported drought periods, then the hypoplasia peaks may be related to factors such as a seasonal increase in parasite load. Other variables such as animal husbandry practices could also be causing these patterns to occur, including the seasonal movement of animals over long distances in search of viable water sources, as part of intra / inter family alliances both in the modern and archaeological material. However, the apparent bimodality of the

hypoplasia peaks, especially as seen on the third molar, would suggest that periodic drought episodes combined with physiological stresses discussed in the previous sections have to be regarded as the most likely cause of the principal patterns of enamel hypoplasia observed in these different ancient caprine populations.

6.6 Conclusions

6.6.1 Interpreting animal husbandry practises

The site of Enkapune Ya Muto clearly stands apart from the other archaeological sites in terms of caprine enamel hypoplasia patterns; it has considerably higher levels of enamel hypoplasia, and unusually goats show more evidence of severe stress than sheep. It is likely that sheep and goats are being herded separately at this site with goats being placed under greater nutritional, environmental, physiological stress than sheep. This suggests animals at this site may have been subjected to a slightly different form of pastorialism than animals at the open plain sites. It is unfortunate that this site contained such a limited number of molars and that the rock shelter site of Maasai Gorge was unavailable for study.

Gifford-Gonzalez (1985) does suggest that Maasai Gorge rock shelter also contained higher numbers of enamel hypoplasia when compared to the open plain site of Narosura. While the enamel hypoplasia from this site was quantified using a different method to that used in this research (number of hypoplasias per mandibular row instead of number of hypoplasias per tooth) and so is not comparable, it does suggest, when combined with the data from this research, that rock shelter sites have higher numbers of hypoplasias than open plain sites. Potentially this indicates that different animal management strategies were being practised at rock shelter sites, compared to open plain sites. This would fit with Robertshaw's (1988) and Ambrose's (1984) suggestions that different economic / pastoral practises were taking place between the different types of site found in the Mau region.

6.6.2 General differences between sheep and goats

As observed in the modern material studied by Balasse, et al. (in press), sheep appear to be under greater stress (as indicated by enamel hypoplasia) than goats in the archaeological assemblages studied. Although there is no obvious difference in enamel hypoplasia frequency between ancient sheep and goats, there is a difference in the types of defects and their severity scores found between the two species, with goats showing fewer severe types of defect and lower severity scores than sheep. It is suggested that variation in the nutritional levels produced by differences in feeding behaviour is the underlying cause for this difference. This clearly demonstrates the importance of nutritional levels on the formation and severity of enamel hypoplasia in caprine populations.

6.6.3 Identifying and interpreting seasonality

In terms of the distribution of hypoplasia on the tooth crown, there seems to be little difference noted between caprines from the archaeological sites, with the majority of enamel hypoplasia being located in the cervical portions of the tooth crown in all populations studied. It is suggested that peaks of enamel hypoplasia on the first molars are related to weaning in the modern and Elmenteitan (Narosura) data-sets. In the Savannah Pastoral Neolithic sites (Lemek North East and Ngmuriak) this peak on the first molar is located more centrally on the tooth cusp and it is suggested that a period of stress immediately following birth may be responsible.

There is some variation between the Elmenteitan and modern data-sets compared to the Savannah Pastoral Neolithic data-set, most obviously on the first and second molars. This may suggest a small degree of difference in the early life management of the animals, causing more stress in the Savannah Pastoral Neolithic populations than the Elmenteitan populations. However, any difference would appear to be small, and may just as likely have been caused by the variety of problems that affect the interpretation of this data, such as variation in growth rates and sheep breeds.

The high frequency of enamel hypoplasia observed in the modern and archaeological domestic caprine herds from southwest Kenya most likely derives from a combination of environmental factors and stress caused by developmental physiology. Physiological events such as weaning appear to be responsible for the peaks occurring early in the animals life, with peaks appearing in the enamel hypoplasia at around 6 months in all populations studied. In the latter part of the dental development, environmental events such as periodic drought episodes brought on by the bimodal rainfall pattern appear to be responsible for the peaks occurring in the hypoplasia distribution. It is suggested that the occurrence of hypoplasia coincides with the two annual dry seasons produced by the bimodal rainfall pattern. Clearly there are also physiological and husbandry practises which may also be exacerbating these environmental stresses, including long distance seasonal mobility and gestation and lactation. Obviously there are several interpretational difficulties which need to be considered, including: the difficulty of establishing the climatic conditions in the mid to late Holocene in Kenya: the possibility that the modern and archaeological Kenyan populations have different growth rates to the modern European populations used to create the development charts applied in this research, and the fact that it cannot be proven that animals were born within the two seasons of birth suggested.

Despite these obvious difficulties, the bimodal distribution in the data appears in all of the populations studied in Kenya. When all of the data is combined the bimodal distribution is still clearly visible, suggesting an underlying signal most likely reflecting a regional pattern in enamel hypoplasia occurrence. It is concluded that this signal is due to the twice yearly dry spells which affect this region and/or long distance seasonal mobility in search of viable water sources.

6.6.4 Summary and future work

The work carried out here and the work published by Balasse, et al. (in press) has clearly demonstrated that the detailed recording and analysis of enamel hypoplasia in sheep and goats has the potential to investigate a range of key archaeological themes:

1) Animal husbandry practises.

Caprine remains from archaeological sites in Kenya have been identified with different or unusual enamel hypoplasia signatures. This has been extrapolated as signatures of seasonal climatic change and/or variation in animal management strategies at these sites. This clearly indicates the potential for enamel hypoplasias to shed more light on differences between rock and open plain sites and potentially even between the Savannah Pastoral Neolithic and Elmenteitan sites in this region of Kenya.

2) Differences between species

This chapter has clearly demonstrated that difference exist between sheep and goats in terms of the frequency, severity and types of defects, enamel and hypoplasia frequencies and suggested these are linked to dietary adaptation. This clearly indicates that enamel hypoplasia can be used to investigate species based differences in archaeological populations in relation to dietary and environmental adaptations.

3) Seasonality

Seasonality, both in terms of physiology, animal husbandry and climate have been clearly shown to impact on the occurrence of enamel hypoplasia. This chapter has indicated the clear potential of enamel hypoplasia to be used in the study of physiological and environmental seasonality within archaeological populations.

4) Future Work

A key area for future research is to identify more precisely the climatic variation and its impact on the rainfall patterns of this region of Kenya. This is essential for the accurate interpretation of patterns enamel hypoplasia potentially related to climatic variation. In terms of the archaeology of the area, a larger study of the region, including more rock shelter and Elmenteitan sites, would be an obvious choice for any future analysis of hypoplasia in this region. Ideally this could be linked to larger scale isotopic analysis of some of the key sites from the region, comparing rock shelter and open plain sites. This would also be useful for establishing any differences in seasonal movements and herding practices, as well as investigating further any differences between the open plain and rock shelter sites. Obviously this could also be tied into a wider study of the enamel hypoplasia from the region, including more rock shelter sites.

7 Archaeological caprines from Iceland

This chapter provides the last of the three geographic case studies of enamel hypoplasia in caprines. In this chapter the interpretations of enamel hypoplasia developed in the previous two chapters in relation to modern populations, are tested on a purely archaeological data-set. The archaeological material derives from the site of Svalbarð on the northeast coast of Iceland. This site has a long occupation sequence, which, for the purposes of this research is divided into two phases: The Medieval Warm Phase (pre-1300 AD) and The Little Ice Age Phase (post-1477 AD). This site is compared to the smaller site of Steinbogi (also from the northeast of Iceland). Steinbogi dates to the intervening period of occupation (late 12th century to early 13th century) and provides an interesting comparison to the site of Svalbarð due to its different environment and its location, inland in the Mývatn region of Iceland.

The chapter provides a short history of Iceland, outlining its settlement, the impact of settlement on the environment and the changing climatic conditions that occurred over the period of occupation of Svalbarð. Caprine enamel hypoplasias are then analysed from the two sites around three research themes: 1) General caprine population level stress with a focus on changing management strategies in the Mývatn region in the 13th century; 2) the impact of deteriorating climate in the second phase of occupation at the site of Svalbarð; and 3) seasonality in terms of changing management strategies and climatic change at Svalbarð.

7.1 Introduction

Iceland is located in the North Atlantic Ocean approximately 60km south of the Arctic Circle. Unlike nearby Greenland, Iceland is considered to be part of Europe although the country is not geologically part of the continental plates of either Europe or North America. Iceland is a geologically very active country, situated on the junction between the Mid–Atlantic ridge-rift zone (Nordel & Kristinsson, 1975). Consequently the use of tephrochronology is an essential tool in the dating of Icelandic archaeological sites (Haflidason, et al. 2000).

7.1.1 Landnám (The Norse colonisation of Iceland)

The Norse colonisation of Iceland began as populations from Scandinavia expanded out into the North Atlantic between A.D. 800 and A.D. 1000 (Vésteinsson, et al. 2002; Amorosi, et al. 1997 Dugmore, et al. 2005). These populations had spread to the eastern island groups of Shetland, Orkney and the Hebrides and the Scottish mainland by ca. A.D. 825. From here the expanding populations spread westwards, colonising the Faros by ca. 860, Iceland by ca. 874 and Greenland by ca. 985 (Amorosi, et al. 1997; Edwards, et al. 2004; Church, et al. 2005).

There are several different sources of varying reliability which are available for the earliest settlements in Iceland. Dicuil's '*De mensura orbis terrae'* written in approximately AD 825 suggest that Christian Monks or hermits had settled on Islands in the North Atlantic, possibly taking sheep with them. It has been suggested that the islands settled were the Faroes, with two settlement periods taking place: a pre Viking period (AD 600 – 700) and then the Viking Landnám (AD 850 – 900) (Jóhansen, 1985). However, this suggestion has not been proved archaeologically and has been disputed by various authors (Buckland, et al. 1998; Arge, 1991; Hansen, 1991). It has also been suggested that the island settled by the monks was Iceland and there are reports of the early Norse settlers in Iceland discovering bells

and crosiers left by these monks (McCririck, 1984). While it is possible that the Christian Monks did settle in Iceland it has not been supported by any palaeoenvironmental or archaeological data (Buckland, et al, 1995, Svenbjarnardóttir, 2002).

Two of the most comprehensive historical sources for the early settlement of Iceland are the Íslendingabók (Book of Icelanders) and the Landnámabók (The Book of Settlement) (Dugmore, et al. 2005). Both are thought to date from the 12th century making neither contemporary with the events they discuss. According to the Landnámabók, Iceland was discovered by an early settler called Naddodd of the Faroe Islands, who was sailing to Norway and got lost. He eventually drifted to the east coast of Iceland and named the country Snæland (Snowland) (Pálsson & Edwards, 1972). The Landnámabók goes on to tell how a Swedish sailor by the name of Garðar Svavarsson also accidentally discovered the country by getting lost and was forced to spend the winter at Húsavík on the north east coast (Pálsson & Edwards, 1972). Garðar Svavarsson was the first to realise the country was an island and renamed it *Garðarshólmi* (literally *Garðar's Islet*). According to the Landnámabók the first person who deliberately sailed to *Garðarshólmi* was Flóki Vilgerðarson, also known as Hrafna-Flóki (Raven-Flóki). Flóki settled for winter at Barðaströnd on the South West coast and re named the island *Ísland* for the drift ice he saw floating in the fjords (Pálsson & Edwards, 1972).

The first permanent settler of Iceland according to the Landnámabók, was the chieftain Ingólfur Arnarson who settled with his family in AD 874. According to the legend, he threw two carved pillars overboard as he neared land, vowing to settle wherever they landed. He then sailed along the coast line until he found them in a place he named Reykjavík (The Smoking Bay) due to the geothermal steam rising from the area (Pálsson & Edwards, 1972). While the exact dates of the earliest Norse settlements in the North Atlantic have been disputed (e.g. Vilhjálmsson 1990; 1991; Hermanns – Auðardøttir, 1991; Olsson 1992; Theodórsson 1998; Hannon & Bradshaw, 2002) the archaeological, palynological and tephrochronological data support the literary evidence in suggesting a 9th century date for the first settlement

of the Island (Dugmore, et al. 2005). All early Viking sites are either cut into or rest directly on top of the landnám teprha, which is dated to 871 $^{+}/_{-}$ 2 (Grönvold, et al. 1995) Once initial settlement had occurred it appears that the rest of the Island was quickly settled in the following decades (Dugmore, et al. 2005).

7.1.2 The Impact of Landnám

The Norse colonisation of the North Atlantic islands had a profound impact on the previously undisturbed environment of the region. The landnám island biota of the North Atlantic was relatively limited, meaning that there were less complex vegetative changes than in more temperate regions with higher diversity (Dugmore, et al. 2005). The presence of woodland areas interspersed with open grass / heath areas meant that many of the regions colonised may have looked familiar to the Nordic settlers. However, despite visual similarities in the land, there were fundamental differences between their Scandinavian homeland and these newly colonised regions. These differences included vital factors such as the inability of the land to produce large quantities of biomass, the seasonal fluctuations in biomass distribution and the sensitivity of the soil to erosion (Dugmore, et al. 2005).

The deliberate introduction by the Norse of domesticated mammals to the regions, as well as accidental introductions such as the mouse, profoundly affected the vegetation and soils of the islands (Dugmore, et al. 2005). The destruction of large areas of woodland is indicated by the decline in birch pollen and the increase in grass pollen on Iceland (Lawson, et al. 2007). This land was presumably cleared to make grazing land for the domesticated animals being imported into the region. This is also supported by the high number of pigs found in the early occupation deposits, suggesting that they may have been utilised to aid land clearance. However, there is debate over the exact extent of deforestation and land degradation caused by landnám. It has been suggested that forest cover was beginning to decline from 3000 BP onwards due to climatic change and that it was not until 1500 AD that the major post settlement decline in vegetation occurred, most probably exacerbated by

overgrazing of the land. The various opposing views on the beginnings of deforestation and soil erosion are covered by: Haraldsson, 1981; Simpson, et al. 2001; Ølafsdóttir & Guðmundsson, 2002; Dugmore, et al. 2000; 2005.

Direct human intervention also caused devastating environmental changes to occur in the region. Activities such as fuel collection, charcoal burning and possibly clearance using fire began the process of soil degradation and erosion (Amorosi, et al. 1997). The deforestation of the region led to the relatively high biomass forests being replaced with low biomass grasslands and heaths. Once under grazing these areas could not support the numbers of grazing animals imported to the region. Unlike the Eastern Atlantic areas, biomass productivity in the North Atlantic is significantly lower, leading to over-grazing and subsequently soil erosion and degradation. It is estimated that in Iceland 90 % of the forests and 40 % of the soil present at 9th century landnám has since been lost (McGovern, et al. 2007).

7.1.3 Palaeoclimatic considerations

Throughout the Norse occupation of the region a number of key environmental changes occurred, including the Little Ice Age. During the Norse expansion into the North Atlantic region in the 9th – 10th centuries it is thought that the region experienced a calmer, warmer and more stable environment than it does today (Amorosi, et al. 1997). While there were still periods of cold within this 'Medieval Warm Period', environmental conditions appear to have been relatively stable. At the beginning of the 14th century the climatic cooling event known as the 'Little Ice Age' began to impact on the subsistence economies throughout the Norse Atlantic region. The full transition of the Medieval Warm Period into the Little Ice Age was complete by 1420 and it has been suggested that this was one of the most 'significant and abrupt (environmental) transitions of the past 6000 years' (Amorosi, et al. 1997: 498).

7.1.4 Norse and Later subsistence and economy

The first wave of settlers (*Landnámsmen*) shared cultural similarities, in terms of political organisation, and a subsistence economy based on domestic animal husbandry and cereal cultivation (Amorosi, et al. 1997; McGovern, 1985; McGovern, et al. 1996). Over time and with geographic separation these 'cultural' similarities between Iceland, Greenland and the Faros diversified, adjusting to the various, environmental and climatic pressures exerted by the different islands (Amorosi, et al. 1997). In the later periods of occupation this produced increasing diversification of the economic strategies. For example, in the later Medieval and Post Medieval periods in Iceland there was growing dependence on marine resources, particularly the exploitation of seal and by the 14th Century there was also increasing reliance on the commercial trading of stockfish with Norway, Germany and England (Outram, 2003).

Iceland's first settler Hrafna-Flóki learnt the hard way that one of the key elements to farming in the North Atlantic was the provisioning of adequate fodder. The Landnámabók tells how Hrafna-Flóki and his men got so distracted with the rich fishing that they made no foddering provisions and over the course of the winter all of their animals died of starvation (Pálsson & Edwards, 1972). In Norse and later societies in the North Atlantic, fodder provisioning was a political as well as economic and environmental variable and farms were rated by their 'fodder reserve value' (Amorosi, et al. 1998). In Iceland it appears that the free-holding farmers were tied into a closely linked system of co-operative independence where the survival of the community took precedent over the survival of individual farmsteads. This local level of co-operation allowed for resources such as common grazing land and sharing of stock and fodder resources to be managed (Amorosi, et al. 1998).

The term fodder does not refer purely to hay. In the ethnographic record there is extensive evidence to suggest the use of seaweed fodder (Hallson 1964; Fenton, 1978 and Kristjánsson, 1978 cited in Amorosi, et al. 1998) Hallson (1964) recorded the use of dried *Rhodymenia palmate* and cooked and dried *Alaria* to feed cattle and

indicated that it was regarded as good quality fodder for fattening animals and producing milk. For the site of Svalbarð it would appear highly like that seaweed was utilized as a fodder source. In the book of Jarðabók (Land register) the entry for Svalbarð dated to August 4th 1712 states *"Grazing land around Svalbarð is tolerable but the grazing at the beach is better"* possibly suggesting seaweed foddering (Amorosi, 1992).

Written records indicate that the earlier settlers brought with them a mixed animal economy with a higher number of cattle than sheep. However, over time the size of the caprine flocks steadily increased while the number of cattle declined **(**Amorosi, 1992; Brewington, et al. 2004; Hambrecht, et al. 2006; Hambrecht, 2007, Harrison, et al, 2008**)**. This shift towards a caprine dominated economy is particularly visible in the northeast regions of Iceland. It has been suggested that this increase in the number of sheep kept was in relation to the shifting climate from the warmer period into the cooler 'Little Ice Age' and a move towards less fodder-dependant animals (Sveinbjarnardóttir, 1992: Amorosi, 1997). It may also be that the decreasing human population of Iceland due to a big epidemic (the Plágan mikla 1402-1404) was also partly responsible for this shift, as sheep require less people to tend for them than cattle (Sveinbjarnardóttir, 1992).

7.1.5 Icelandic sheep

While there are no modern populations of Icelandic sheep used in this research, the breed has remained virtually unchanged since the animals were first introduced by the Norse settlers (Thorgeirsdottir et al. 1999). Icelandic sheep or *Íslenska sauðkindin* are one of the world's oldest and most pure breeds. (http://www.bcsba.org.uk/coloured-sheep/icelandic-sheep.html). They belong to the same group of sheep as the animals from Orkney – the Northern Short Tails. Icelandic sheep are medium-sized animals (although the largest of the Northern Short Tail breeds) with short legs and stocky build (see Figure 7.1) and like the other primitive breeds discussed they come in a variety of fleece colours

(http://www.icelandicsheep.com/qfacts.html). Icelandic sheep are more like goats in their feeding habits, preferring to browse over a wide range of plants, often seeking out weeds over grass in pastures. This makes them ideally suited to the hilly, harsh terrain and rough grassland and pastures found in Iceland (http://www.icelandicsheepinwales.co.uk/).

Figure 7.1: Icelandic Sheep (From: http://www.icelandicsheep.com/Saddleback.htm).

7.2 The Archaeological Sites

While there were some small comparative caprine assemblages available from sites around Iceland, the largest and most useful data sets were those from Svalbarð and Steinbogi.

7.2.1 Svalbarð

The site of Svalbarð is located in the south-western coastal region of the Svalbarðshreppur in the north east of Iceland. The excavation of the site focused on the large midden from a very active and rich farmstead located beside the river Svalbarðsá (Amorosi, 1992). Historically the earliest record of the site is from 1318 although this appears to be a relatively late date for the earliest settlement at the site. Archaeologically, the earliest evidence for the settlement dates to the 11th century AD based on the types of artefacts recovered. The site has a very long occupational stratigraphy, covering over eight centuries (*c.*1050 – 1880 based on artefact typographys), including the transition between the Medieval Warm period and the Little Ice Age (Amorosi, 1992).

The site was one of the largest and economically most productive farms in the region. Historical records indicate that the site held extensive grazing lands and hayfields along the river's flood plain. The site also had multiple *sels* (sheilings) including the extremely productive coastal sel of Hjalmarsvik which had rich grass and plentiful seaweed fodder (Woollett, 2008). The archaeological data from this site, including the faunal assemblage, suggest that the north-eastern part of Iceland suffered a particularly stressful period during the climatic cooling associated with the onset of the Little Ice Age (Amorosi, 1992). The cattle to caprine ratios shift from 1 cow: 4-5 caprines to 1 cow: 6-7 caprines. This change in the ratio of cattle to caprines may reflect an increasing emphasis on wool production and potentially a move to less fodder-dependant animals, reflecting the increasingly poor environmental conditions. There is also an increase in the number of young lambs

found in the assemblage in the later periods, suggesting that the climatic changes were directly impacting the mortality of animals, particularly during early spring when they were giving birth and sea ice would have been at its maximum extent (Amorosi, 1992).

As the site analysis is incomplete, exact dates and phasing were unavailable for the samples collected as part of this research. However, the stratigraphic depths of the samples from within the midden were available. The lack of dates for the samples was overcome by dividing the site into two phases based on a single clearly identifiable burnt deposit (Stratigraphy Unit 8) which ran through the centre of the midden deposit, samples were then located in relation to this deposit. This deposit provided a clear dividing line through the chronology of the site allowing the samples to be divided into two distinct chronological periods: Svalbarð 1, dating to the Medieval Warm period and Svalbarð 2, dating to the Little Ice Age period. The midden deposit was very clearly stratified with several tephra layers running though the deposits, including two key tephra layers, one immediately above Stratigraphic Unit 8 and the other immediately below it. Early dating of the site identified these tephra as Hekla 1693 and Veiðavötn 1717 (Amorosi, 1992, 1996). However, more recent analysis carried out on this site has produced significantly different dates for these two tephra, identifying them as Hekla 1300 and Veiðivötn 1477 (Woollett, 2008). Based on these dates the early period of the site (pre-1300) can be dated from approximately 1050 to 1300, and the later period of the site (post-1477) can be dated from 1477 to 1880.

7.2.2 Steinbogi (SBO)

Steinbogi is a small late 12th - early 13th century farmstead of probably low economic status from the Mývatn District, of northern Iceland. The faunal collection was dominated by caprines nearly all of which were probably sheep. The ratio of cattle to caprine bones in the collection is approximately 1: 22 (Brewington, et al. 2004). This is very different from the pre-13th century assemblages from this region where the

cattle: caprine ratio is around 1:3. However, this does fit with the general trend in the north of Iceland by the 18th century of large number of sheep compared to cattle. The Mývatn region by the 18th century is known as the sheep raising region, reflecting the high numbers of sheep found there. The age-at-death data for caprines at Steinbogi indicates that the majority of animals survived past 2 years of age with 20-30% reaching 4 to 5 years of age. There is a small peak of deaths at around 7-10 months which may be related to autumn stock killing in preparation for the winter months. The overall pattern suggests a wool-producing economy with animals also being used for the secondary by-products of meat and milk (Brewington, et al. 2004). The two sites are compared in Table 7.1 below and their locations are shown in Figure 7.2.

Site	Date	Climatic period	Location	Economic status	Cattle: Sheep
Svalbarð pre-1300	1050 to 1300	MWP	NE Iceland	High	1:4
Svalbarð post-1477	1477 to 1880	LIA	NE Iceland	High	1:7
Steinbogi	12th to 13th centuries	MWP	NE Iceland	Low	1:22

Table 7.1: Table comparing the archaeological sites studied in Iceland, MWP = Medieval Warm Period, LA = Little Ice age.

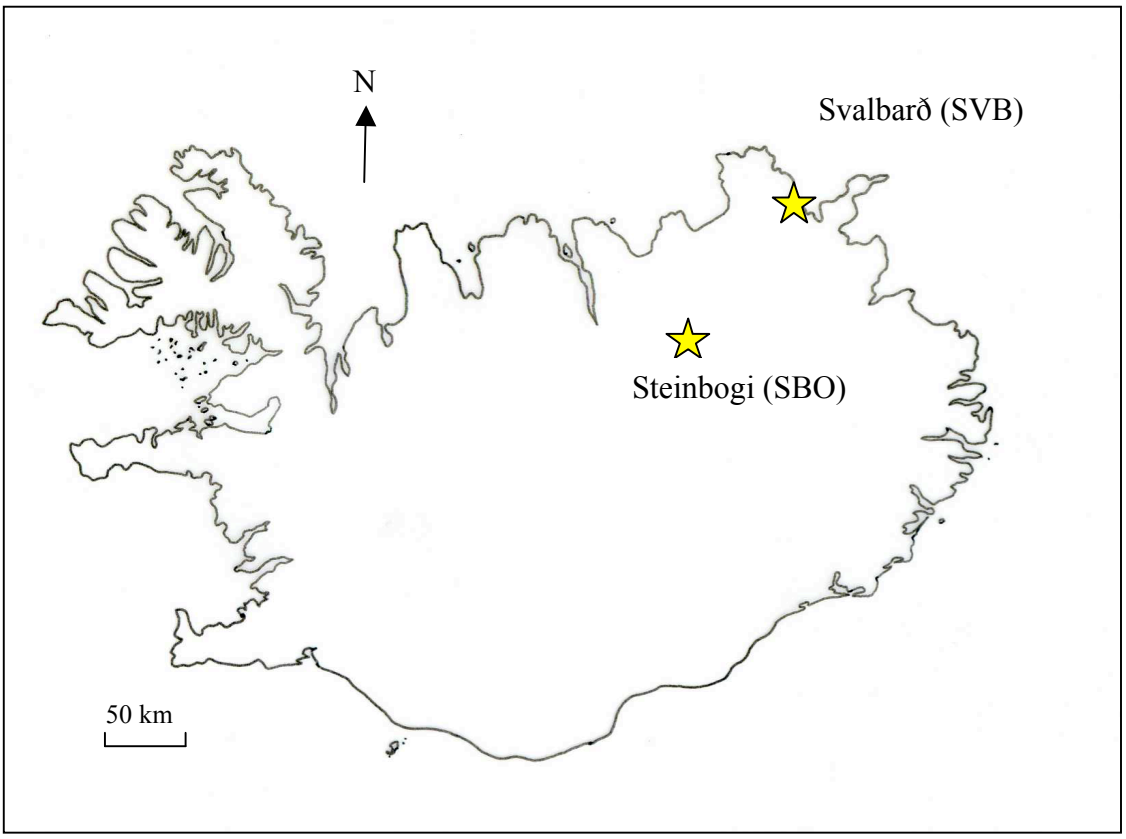

Figure 7.2: The locations of the two sites studied in Iceland.

7.3 Key Research Themes

The previous two chapters developed methods and ideas for the interpretation of enamel hypoplasia using modern material to provide a baseline for archaeological samples. Using the baselines created in these earlier chapters, this chapter attempts to investigate the practical application of the study of enamel defects in purely archaeological populations. With this in mind, very similar research themes are addressed in this chapter, but with a focus on the archaeological interpretation and context of sites studied.

General levels of population stress

This theme continues the research of the previous two chapters, using enamel hypoplasia to identify general stress levels in populations and their causative factors. The two sites of Steinbogi and Svalbarð are compared in terms of the frequency of caprine enamel hypoplasia, with a focus on the impact of status, environmental change and shifting animal husbandry practices in the 13th centuries in the Mývatn region of northeast Iceland.

Climatic change

Using enamel hypoplasia as a general indicator of stress levels as discussed in previous chapters, climatic deterioration associated with The Little Ice Age is explored (particularly at the site of Svalbarð). Suggestions (provided by previous research on faunal assemblages from Iceland) that the northeast of the island was more severely affected by climatic fluctuations than other parts are also explored.

Seasonality

Seasonal nutritional fluctuations, specifically related to foddering practices, climate change, and shifting subsistence strategies will be explored at the site of Svalbarð.

7.4 Results

A total of 173 isolated teeth and mandibles were collected from Svalbarð, of these 95 mandibles and isolated teeth were selected for study, based on the criteria discussed in Chapter 4. This produced a total of 166 molars for study. The site of Steinbogi produced a total of 40 teeth. Of the 166 molars from Svalbarð, 140 were complete and fully formed and 26 were still forming. Steinbogi produced a total of 33 complete teeth and 7 incomplete teeth. Of the incomplete teeth recorded from Svalbarð only 8% (2 out of the 21) had evidence of enamel hypoplasia and none of the incomplete teeth from Steinbogi produced enamel hypoplasia. As in previous analyses, incomplete teeth have been excluded from further analysis due to the low numbers of incomplete crowns showing evidence of enamel hypoplasia and the difficulties of relating teeth that have a root enamel junction (REJ) to those without an REJ. The summary data is shown in Table 7.2.

	Svalbarð	**Steinbogi**
Total complete teeth	140	33
Total no. hypoplasia recorded	197	49
% of complete teeth with hypoplasia	70%	58 %

Table 7.2: Comparison of the two archaeological sites from Iceland in terms of enamel hypoplasia.

7.4.1 General levels of population stress

Key points

- Overall Svalbarð has a higher frequency of enamel hypoplasia than the site of Steinbogi.
- There were no observed differences between the two sites in terms of the severities of the enamel hypoplasia.
- Overall Steinbogi has a higher number of line defects compared to Svalbarð.

General results

The data is shown in Table 7.3 and Figure 7.3 to Figure 7.5. Seventy percent of the complete teeth from Svalbarð showed enamel hypoplasia, amounting to a total of 197 hypoplastic events. The defects affected 56% of all first molars, 83% of all second molars and 80% of all third molars. For teeth showing evidence of enamel hypoplasia, there was an average of 1.3 defects per first molar, 2.5 defects per second molar and 2 defects per third molar. Of all the defects recorded 120 (61%) were line-type defects, 51 (26%) were depression and 26 (13%) were pit-type defects. Of the line-type defects 42 % had severity score one, 39 % were severity score two, 6% were score three and 15 % were score four.

At Steinbogi, 58 % of the complete teeth studied had enamel hypoplasia. Defects affected 51 % of first molars, 27 % of second molars and just 21 % of third molars. This low score for the third molars is more likely due to the limited number of third molars available for study (only 7) than a true reflection of the number of teeth affected by enamel hypoplasia. Of the 49 enamel defects recorded at the site of Steinbogi 41 (84 %) were line-type defects, 6 (12 %) were depressions and 2 (4 %) were pits.

	Svalbarð (n=197)	**Steinbogi (n=49)**
% of line-type defects	61 %	84 %
% of depression-type defects	26 %	12 %
% of pit-type defects	13 %	4 %
	Svalbarð (n= 120)	**Steinbogi (n= 41)**
% of line-type severity score 1	42 %	93 %
% of line-type severity score 2	39 %	7 %
% of line-type severity score 3	6 %	0 %
% of line-type severity score 4	15 %	0 %

Table 7.3: Comparison of the two archaeological sites from Iceland in terms of defect type and severity.

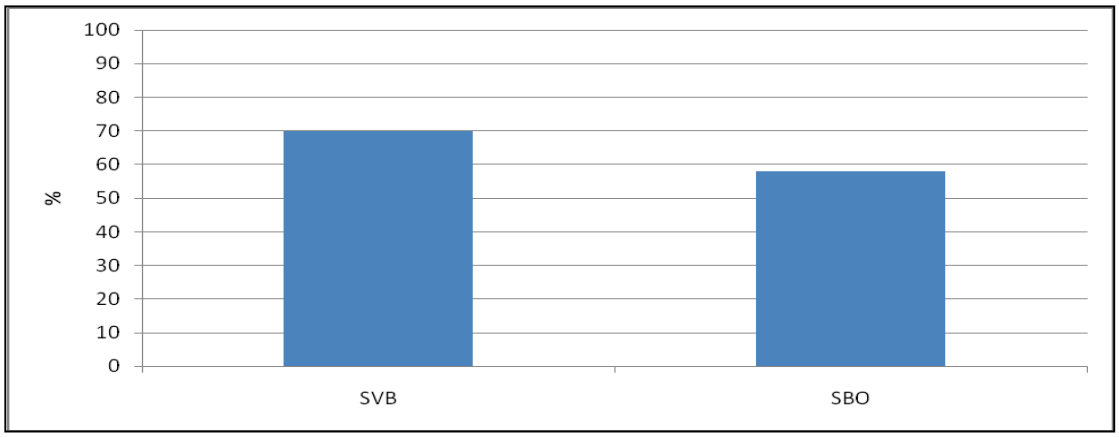

Figure 7.3: Comparing the percentages of complete teeth with enamel hypoplasia across the Icelandic sites. (SVB = Svalbarð, SBO = Steinbogi).

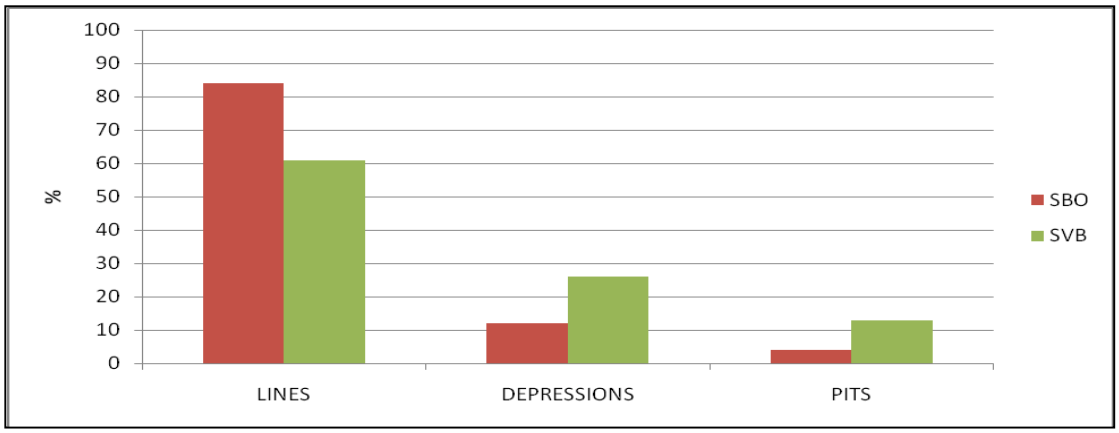

Figure 7.4: Comparing the percentages of different hypoplasia types between the Icelandic sites. (SVB = Svalbarð, SBO = Steinbogi).

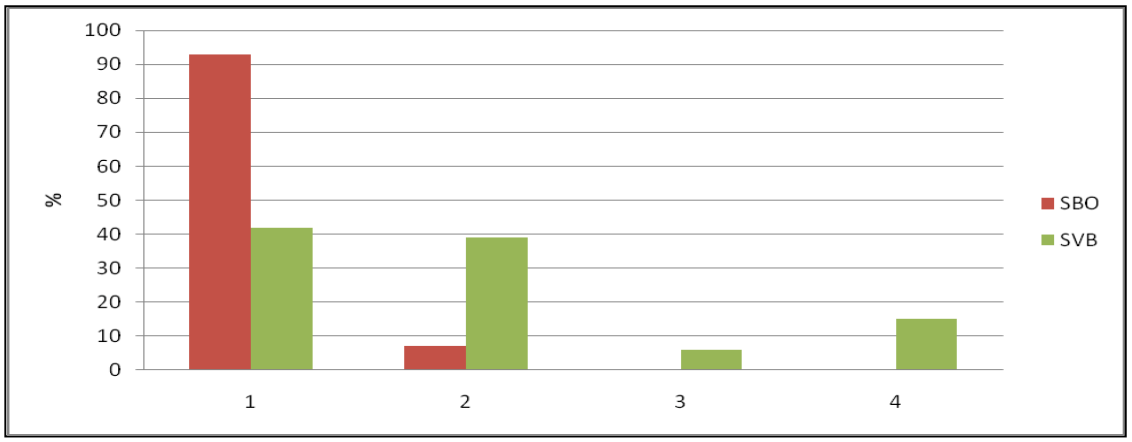

Figure 7.5: Comparing the percentage of different defect severity scores between the Icelandic sites. (SVB = Svalbarð, SBO = Steinbogi).

7.4.2 Climatic change

Key points

- There is no statistical difference between the two climatic phases at Svalbarð in terms of number, type or severity of enamel hypoplasia.

General results

When the two phases at Svalbarð are compared (pre-1300: The Medieval Warm period and post-1477: The Little Ice Age period) there is no statistical difference in the frequency, severity levels and types of enamel hypoplasia found on the caprine teeth (see Tables 7.4 & 7.5 and Figure 7.6 to Figure 7.8).

	Pre-1300	**Post-1477**
Total complete teeth	83	57
Total no. hypoplasia recorded	112	85
% of complete teeth with hypoplasia	69%	71 %

Table 7.4: Comparison of the two phases from Svalbarð in terms of enamel hypoplasia.

	Pre-1300 (n=112)	**Post-1477 (n=85)**
% of line-type defects	63%	58%
% of depression-type defects	22%	31%
% of pit-type defects	15%	11%
	Pre-1300 (n=71)	**Post-1477 (n=49)**
% of line-type severity score 1	42%	39%
% of line-type severity score 2	38%	37%
% of line-type severity score 3	7%	8%
% of line-type severity score 4	13%	16%

Table 7.5: Comparison of the two phases from Svalbarð in terms of defect type and severity.

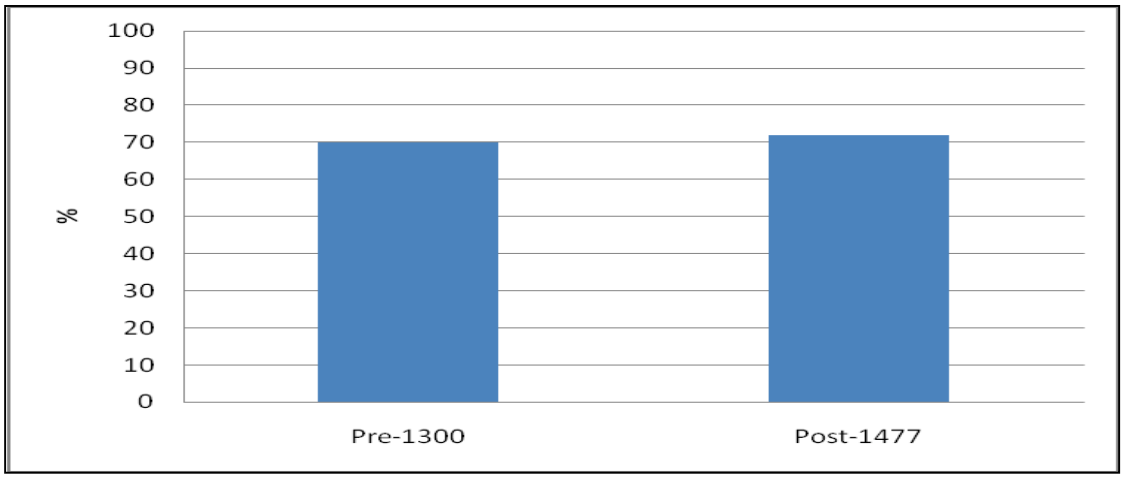

Figure 7.6: Comparing the percentages of complete teeth with enamel hypoplasia between the two climatic periods at Svalbarð.

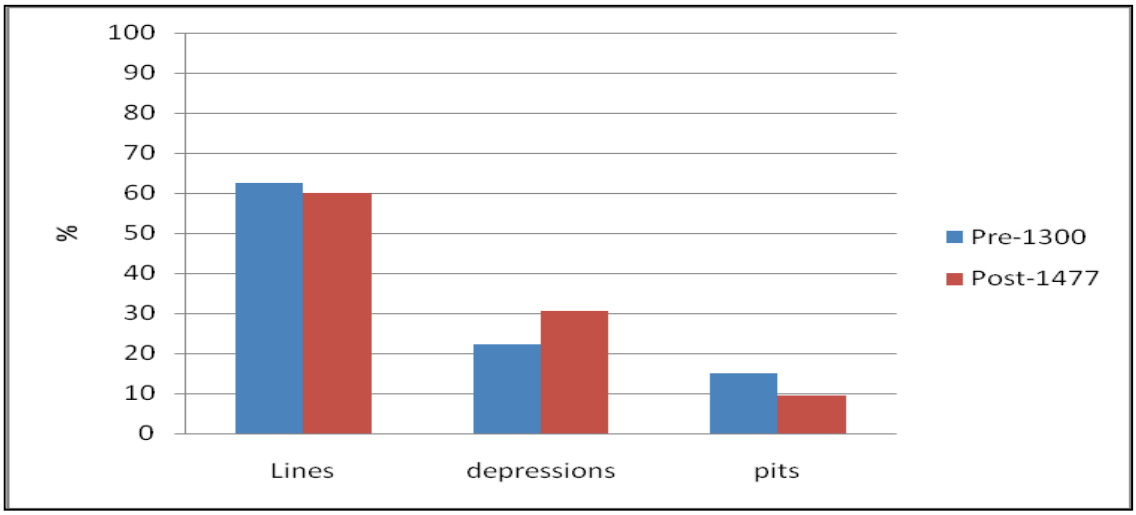

Figure 7.7: Comparing the different types of defect between the two climatic periods at Svalbarð.

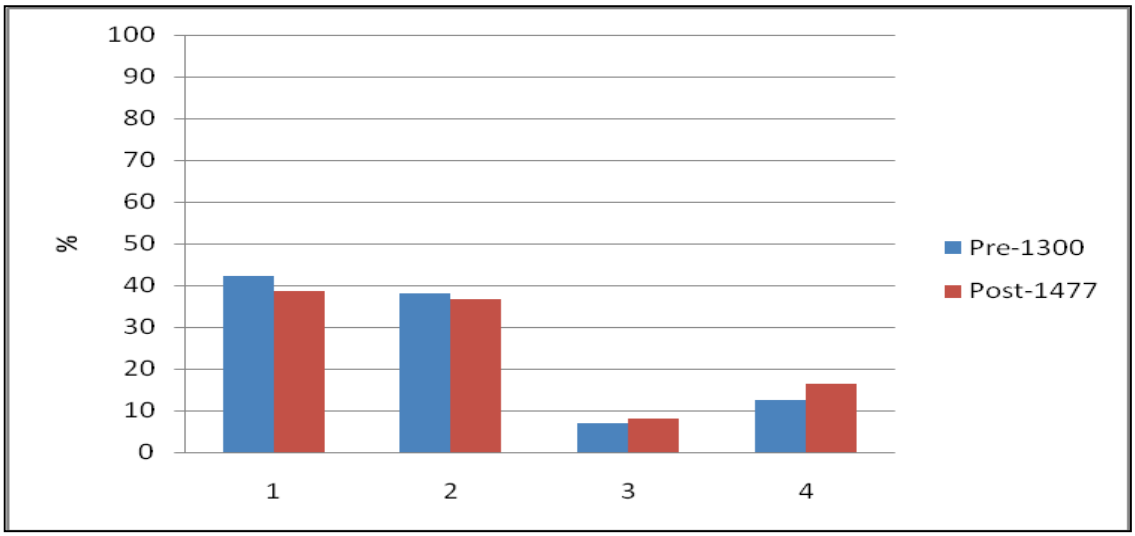

Figure 7.8: Comparing the defect severity levels between the two climatic periods at Svalbarð.

7.4.3 Seasonality

Key points

- Hypoplasia occurs in the cervical half of all three molars in the both the Svalbard and Steinbogi populations.
- There is a slight variation in the timing of the enamel hypoplasia peaks on the second molar between the two phases at Svalbarð.

General results

The distributions of enamel hypoplasia on the anterior and posterior cusps of the Svalbarð population are shown in Figure 7.9. At Svalbarð, defects on the first molar are exclusively located in the cervical 25 millimetres of the tooth crown, with the majority of defects located in the 21 millimetres of the crown above the root enamel junction (REJ). A very similar pattern is seen on the second and third molars, with the vast majority of defects located in the cervical half of the tooth. On both the second and third molars there are very few defects located above 19 millimetres from the REJ. The distribution of enamel hypoplasias from Steinbogi are shown in Figure 7.10, although the numbers are small - rendering accurate comparisons difficult - they appear to follow the same pattern as all other populations studied as part of this research – i.e. enamel hypoplasia occurring in the lowest half of the tooth crown.

The data from the two periods at Svalbarð was analysed by calculating running means on relative frequency values (as discussed in Chapter 4). Unfortunately, the numbers of enamel hypoplasias recorded in the Steinbogi population were too small to be included in this analysis. Results for the Svalbarð population is shown plotted against crown development, the pre-1300 population is shown in Figure 7.11 and the post-1477 population in Figure 7.12. As expected, in both climatic periods a peak of enamel hypoplasia is seen occurring at the time of birth. In the pre-1300 population there is a second peak of enamel hypoplasia occurring at approximately 6 months after birth. This second peak is not visible in the post-1477 population; instead here

there are an almost continuous number of defects in the months immediately following birth until approximately 5 months.

In the second molar there is a single peak of enamel defects occurring in both the pre-1300 and the post-1477 populations. In the pre-1300 population, this peak begins to develop around January (10 months after birth) building to a maximum peak in March and April. In the post-1477 population the peak follows a very similar pattern, beginning in January and continuing until it peaks in May / June. A similar pattern is seen in the third molar, with a single peak of enamel hypoplasia occurring in both populations. The peak begins slightly earlier than that seen in the second molar and peaks in May / June in both populations. The peak seen in the third molar in the post-1477 period is not as clearly defined as the peak on the third molar in the earlier population.

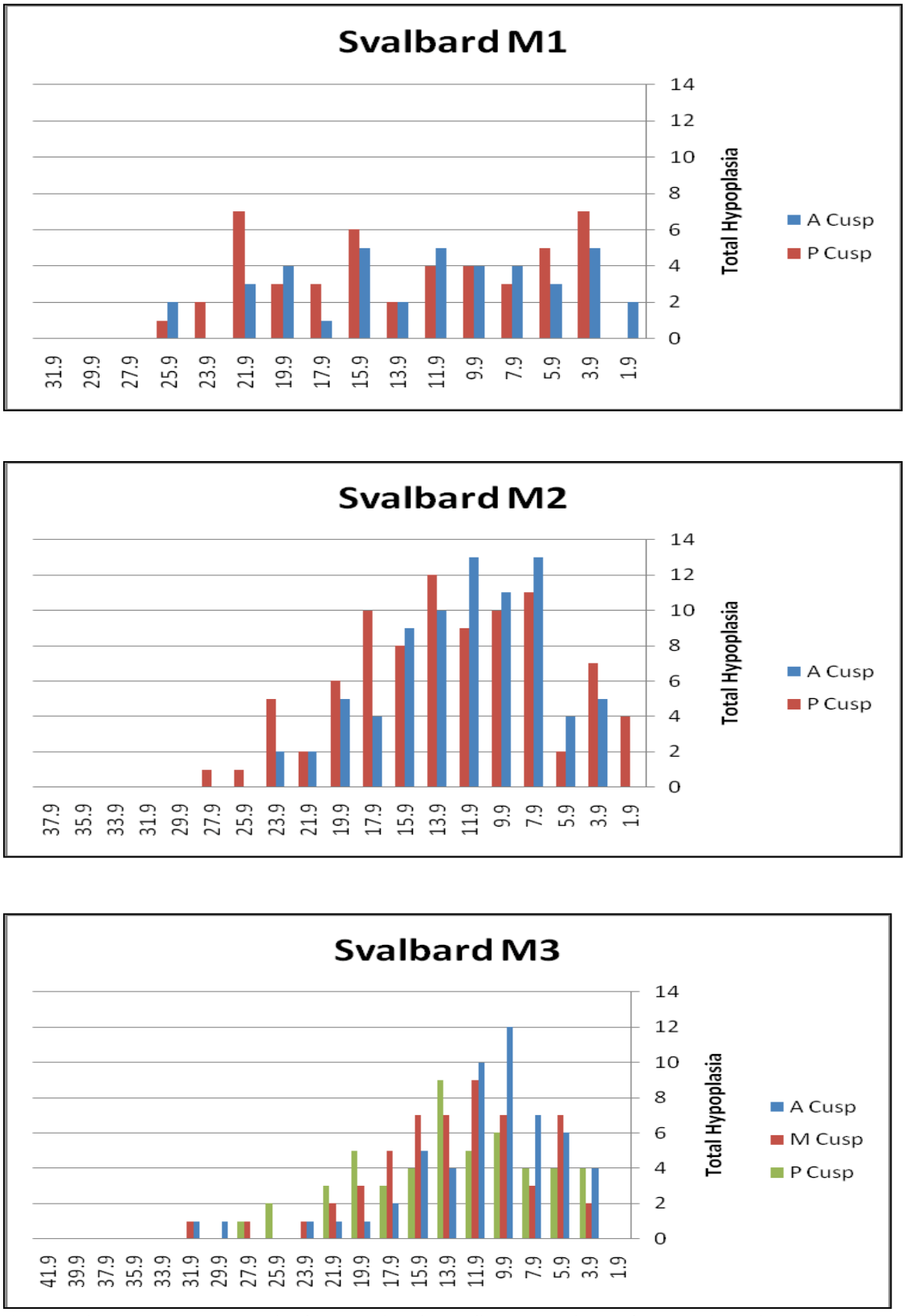

Figure 7.9: Enamel hypoplasia frequencies from Svalbarð (2mm frequencies with the root-enamel junction on the left and the maximum height of the tooth crown on the right). A = anterior, M = middle, P = posterior.

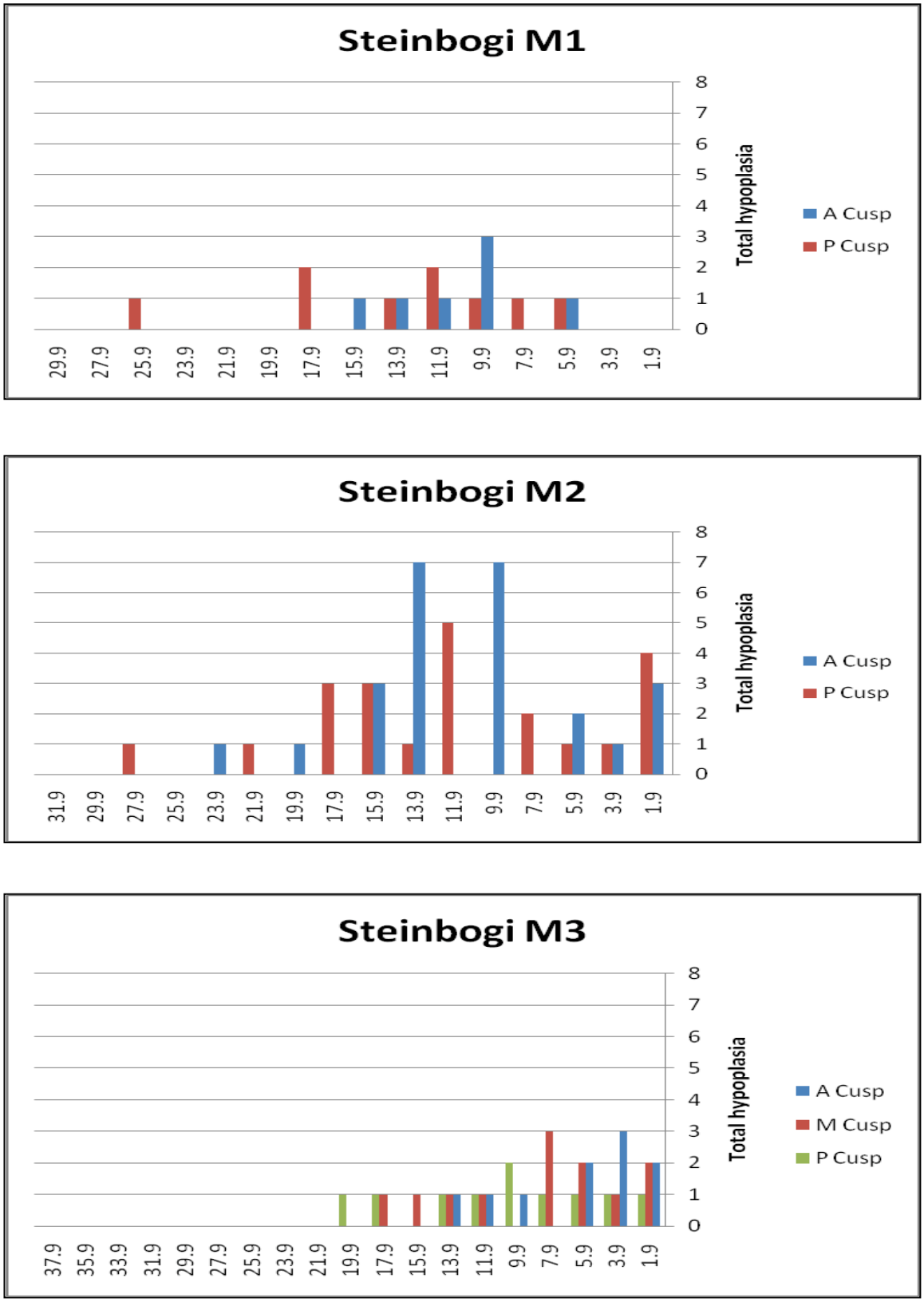

Figure 7.10: Enamel hypoplasia frequencies from Steinbogi (2mm frequencies with the root-enamel junction on the left and the maximum height of the tooth crown on the right).
A = anterior, M = middle, P = posterior.

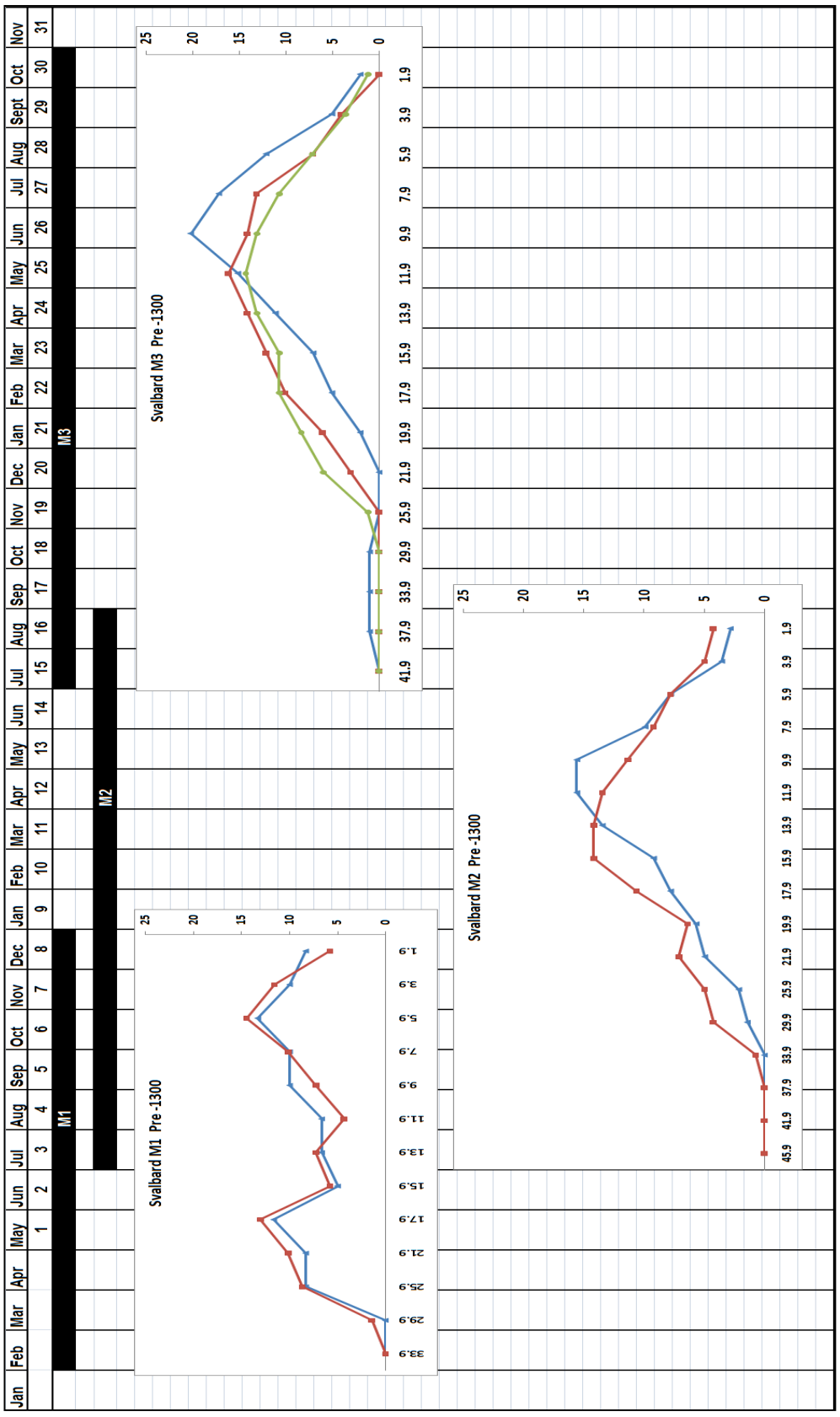

Figure 7.10: The adjusted data from Svalbarð pre-1300 plotted onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.

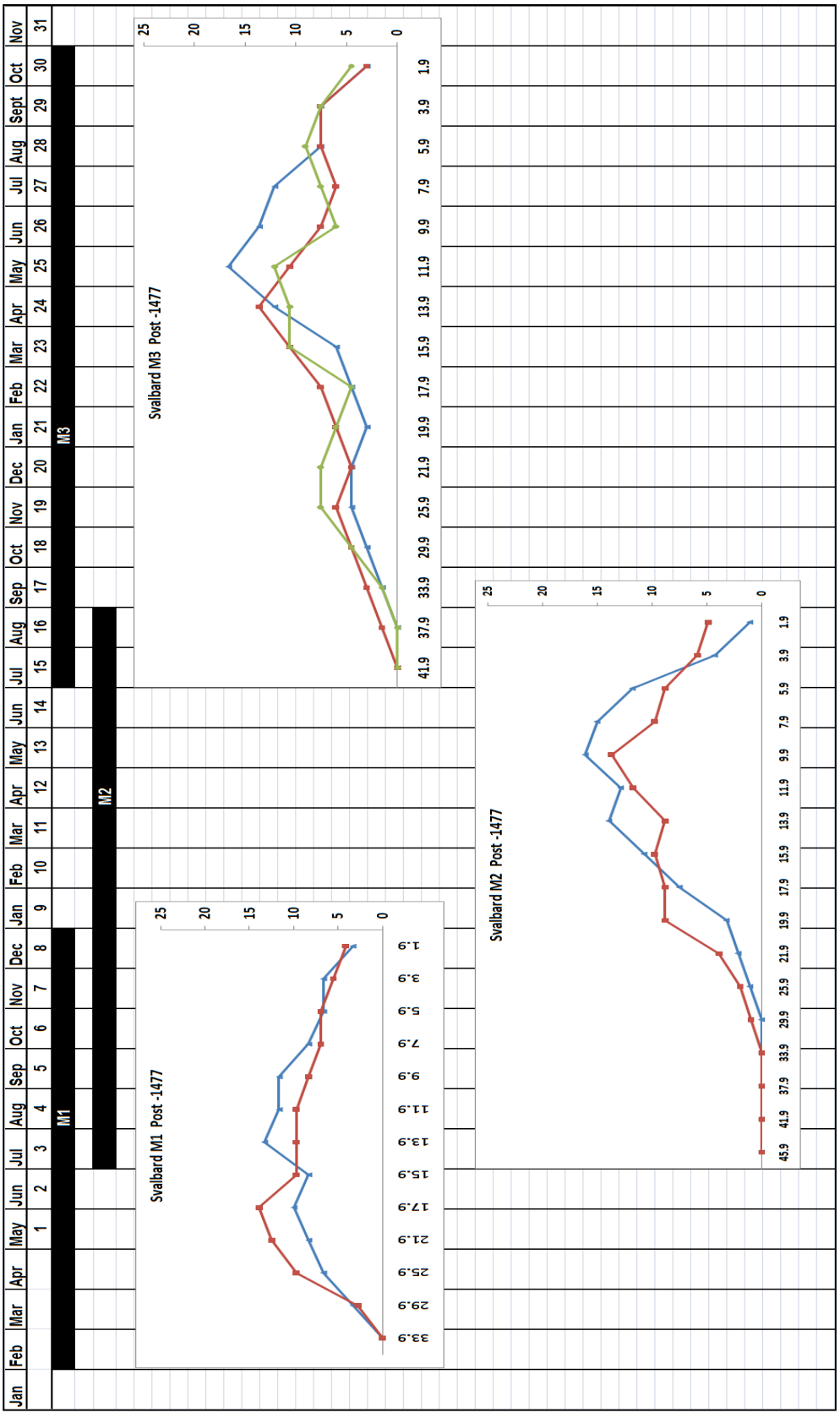

Figure 7.11 The adjusted material from Svalbarð post-1477 plotted onto a chart of tooth development rates. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.

7.5 Discussion

7.5.1 General levels of populations stress

In terms of the frequency of enamel hypoplasia, the site of Svalbarð has a higher overall frequency of defects than the site of Steinbogi but there are no differences seen between the two sites in terms of the severity scores of enamel hypoplasia. The only other real difference noted between the sites is in the distribution of defects types, where Steinbogi has a higher number of line defects.

As discussed in Chapter 3, linear type defects indicate more abrupt and severe periods of stress, while depressions (although needing to be treated with caution, as discussed in Chapter 5) represent milder, longer periods of stress. The high frequency of defects seen at Svalbarð may be a reflection of the more challenging environmental conditions found in the far north of Iceland. Whilst the site of Svalbarð has a higher frequency of enamel hypoplasia than Steinbogi, when the types of defects present are compared, Steinbogi has a higher number of line-type defects with Svalbarð on the other hand having more depression-type defects. This suggests that the animals from Svalbarð may have experienced more long-term, mild, periods of stress than those from Steinbogi. The Steinbogi population, appeared to suffer from more abrupt, moderate level, stress events with limited numbers of long term, mild events, indicated by the high number of line-type defects and the low number of depression-type defects.

The high number of line-type defects in the Steinbogi population may be a reflection of the more challenging northern environment as suggested for the high frequency of defects in the Svalbarð population. While Svalbarð (situated on the coast), experiences long cold summers, it has milder winters than Steinbogi (situated inland), which suffers from extremely cold winters with milder summers (see Figure

7.12, Tveito, et al. 2000). As shown in Figure 7.12 average summer (July) temperatures are higher inland at Steinbogi than on the coast, while average winter temperatures (October) are better on the coast at Svalbarð and colder inland at Steinbogi.

The higher number of line-type defects seen at Steinbogi may be a reflection of these extreme winters. Alternatively, there are several other factors which must be considered for the Mývatn region, including the rate of environmental degradation, changing animal management strategies and the economic status of Steinbogi. There have been numerous articles written on the environmental impact of landnám on the pristine environment of Iceland (e.g. Amorosi, et al. 1997; Dugmore, et al. 2000; 2005; Lawson et al. 2007). However, the environment of the Mývatn district, certainly in the periods preceding the occupation of Steinbogi (9^{th} – 12^{th} centuries when the earlier farms such as Sveigakot and Hofstaðir were occupied), appears to have been well managed, with little evidence of the immediate environmental degradation and erosion that has been suggested for other parts of Iceland (Mc Govern, et al. 2007). A wide ranging land survey carried out in the area has in fact begun to overturn many of the assumptions about the human impact on the environment of Iceland.

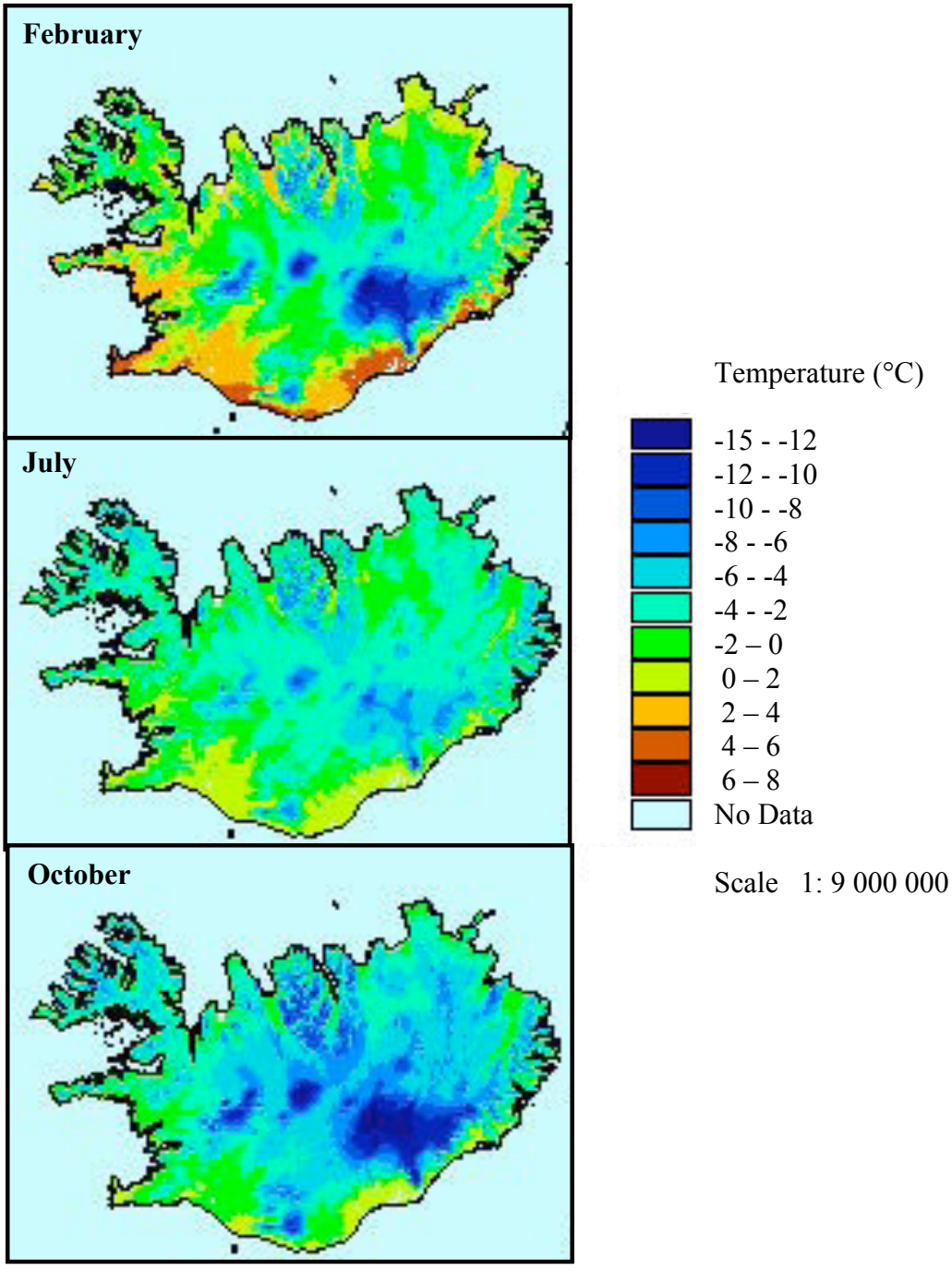

Figure 7.12: Average monthly temperature in Iceland between 1961 – 1990 (After Tveito, et al. 2000).

The study by McGovern, et al. (2007) suggests the speed of the environmental impact was considerably slower in this region than has been previously assumed. Relatively large stands of birch trees were still present in Mývatn several centuries after landnám (Lawson, et al. 2007) and the extensive wildfowl populations in the area appear to have been carefully managed (McGovern, et al. 2006). It is not until the mid 10th century that extensive deforestation is evident along with accompanying soil erosion. It even appears that there was a possible attempt to slow the rate of animal-induced deforestation and soil erosion as the faunal records indicate that pig and goat numbers had been reduced at least a century before pollen evidence shows effective deforestation to have taken place. Steinbogi was occupied in this period of environmental change, when extensive deforestation of the region had occurred and when soil erosion would have been becoming a problem. This potentially would have placed a lot of pressure on the farm in terms of fodder supplies and reserve management, as summer grazing lands became degraded deserts.

Steinbogi is the only site from the Mývatn region that dates from the period of transition in animal management strategies suggested by the faunal record. Earlier sites (9th-12th centuries) from the region such as Sveigakot and Hofstaðir have wide ranges of species present, including pigs and horses. These early sites also have a caprine to cattle ratio of approximately 2:1 (McGovern, 2003). In the farms from the later periods of occupation, the economy has shifted towards the caprine dominated patterns seen in the 18th century Jarðabók farms. Caprine remains dominate these later faunal assemblages, with caprine to cattle ratios as high as 24:1, leading to its description as the sheep producing region (McGovern, et al. 2007; McGovern, 2003). Analysis of these later sites has indicated that the sheep in this region were kept for mixed economic reasons, but with a focus on wool production (McGovern, 2003; Brewington, et al. 2004). The site of Steinbogi fits with this economic model, indicating that the transition of agricultural practices to the intensive wool production backed by dairying economy (as modelled by Ingimundarson, 1995 for the Common Wealth periods) was already in motion in the 13th century.

While the immediate environment of Steinbogi may appear to have been well managed in the Mývatn region, the increasing climatic instability of the area in the 13th century, combined with the beginnings of deforestation, land remodelling and the introduction of new stock-raising strategies, would have potentially placed an extreme amount of pressure on the farms. McGovern (2007) suggests that this combination of factors could have easily led to crucial miss-timings for land management, causing sub-optimal winter grazing and over-grazing of the uplands. The higher number of line-type defects seen at Steinbogi may reflect this transition with increased levels of stress associated with the introduction of a more intensive sheep production system to the Mývatn district, as well as the beginnings of land degradation and miss-management. These factors combined with the extremely cold winters potentially caused the high numbers of moderate impact, short term physiological stress events seen in the Steinbogi caprine population. The population from Svalbarð on the other hand - with its higher numbers of depression-type defects - may represent the longer more drawn out cold seasons, leading to periods of fodder shortages caused by reduced growing seasons.

The site of Steinbogi is also considered to have been a relatively low status settlement based on its small size and its location on a relatively steep slope exposed to both the north and east winds. This potentially is another factor in the variation of enamel hypoplasia patterns seen between this site and the relatively high status site of Svalbarð, given the complicated politics of fodder and resource management (as discussed in section 7.1.4). The concept of the *hreppur* (15 – 30 neighbouring farmsteads linked into a system of co-operative interdependence) provided a minimum level of joint resource management, including stock and fodder sharing. While this level of local co-operation was the source of the adaptive resilience seen in rural medieval communities in Iceland, the risk would not have been spread evenly throughout the community, often benefiting the wealthiest farms (Amorosi, et al. 1998). This combined with local variations in drainage, slope and erosion rates

meant that variation in climate could produce dramatically different farm survival rates within the same region (Olafsdottir & Guðmundsson, 2002). This can still be seen in the Mývatn region, where the pastures are still green around the site of Hofstaðir and yet other areas are completely degraded into the subarctic deserts as seen around the site of Sveigakot (Simpson, et al. 2004; Thomson & Simpson, 2006).

There are clearly many factors which potentially impacted on the animals from Steinbogi. It is suggested that a combination of new animal husbandry regimes related to the shifting animal economy, the beginnings of environmental degradation and possible complex community survival strategies may all have impacted on the Steinbogi animals, leading to their high numbers of linear type enamel defects. There has been a large amount of work carried out in the Mývatn region of Iceland looking at many of these factors. Ideally a much larger selection of sites from this region of Iceland could be studied, allowing a more integrated approach to the study of enamel hypoplasia with the detailed climatic, environmental and social studies that have been carried out in the region.

7.5.2 Climatic change

Throughout the Norse occupation of Iceland the climate deteriorated as the shift from the 'Medieval Warm Period into the 'Little Ice Age' began. There has been much dispute between scholars about the exact meaning of these two terms as well as the definitions of their beginning and end dates (see Ogilvie & Jónsson, 2001; Grove, 1988; 2001; Hughes & Diaz, 1994 for general overviews). Scholarly debate aside, there is circumstantial climatic evidence from Iceland to suggest that conditions were generally mild and stable until the mid to late 12th century and that from that date onwards to the 16th century there were relatively short periods of harsh climatic conditions (Ogilvie, 1991, 1998). Data from the Greenland Ice sheets has been used to reconstruct a variety of detailed climatic models for the region. These have demonstrated a wide range of climatic variation in the past climatic record, including temperature, storminess, snow accumulation rates and atmospheric circulation patterns (e.g. Johnsen, et al. 1992; Mayewski, et al. 1993; Mayewski, et al. 1994; Chappellaz, et al. 1993; O'Brian, et al. 1995; Meeker & Mayewski, 2002; Dawson et al. 2003). There has also been much discussion of the exact impact of this changeable climate on the medieval settlements of the North Atlantic (e.g. Barlow, et al. 1997; Jennings, et al. 2001; Dugmore, et al. 2007; Mc Govern, et al. 2007).

McGovern, et al. (2007) suggests that it is the climatic unpredictability caused by this highly variable climate, rather than a steadily worsening climate, that caused problems for the Norse settlers. Northern societies are often resilient to a wide range of climatic variability as the demographic records for early Iceland reveal, with population demographics remaining stable even in the face of severe cold and violent volcanic eruptions (Vasey, 1991; 1996; McGovern, et al. 2007). The early medieval law codes and annals from Iceland also clearly indicate that there was an awareness of climatic variability as well as the close relationship between grazing pressures and animal welfare (Gudmundsson & Thorhallsdóttir, 1999; Ogilvie, et al. 2000).

McGovern, et al. (2007) suggest that the inability to predict and anticipate key variables such as the end of the growing season in upland pastures, led to the extensive soil erosion and land degradation which ultimately caused the failure of many of the Norse settlements.

The fact that there were no differences observed in the caprine enamel hypoplasia records between the two periods at Svalbarð is intriguing. It was expected that the increasingly deteriorating and unpredictable climate would be visible in an increasing frequency and severity of enamel hypoplasia. The fact that it is not raises some interesting possibilities. It must be remembered that the presence of enamel hypoplasia indicates survival; potentially the climatic impact was so severe that many animals died before recording the severe events in their enamel. However, this scenario would appear unlikely, as mass mortalities like this should be clearly visible in the age profiles constructed for the ancient flocks.

While there are no obvious mass mortalities in older animals Amorosi (1992) suggests that the sharp increase in the numbers of neonatal bones in the later assemblages may reflect short term poor weather events. Cold spells are a well documented cause of mass mortality in neonatal lambs from the 16th century Iceland (Ogilvie 1981). Given the location of the sheep houses and lambing areas at Svalbarð, along the shoreline, Amorosi (1992) suggests that increasing sea ice levels in the spring lambing season could be responsible. This suggests that the flocks were adversely affected by the changing climatic conditions, but that the spring lamb mortalities are the only evidence of this. It is possible that with good management, adequate shelter provisions, and advance planning to keep fodder supplies constant, the climatic impact on these animals was limited if they survived past their first months. This would suggest that the farm at Svalbarð was well-managed and flexible in its approach to the changing climatic conditions.

This hypothesis is supported in the shifting faunal signatures seen at the site, for example the increasing reliance on marine resources. In the later periods of occupation at Svalbarð there are dramatic increases in the numbers of shellfish (recorded by the Svalbarðshreppur as famine food) as well as increasing reliance on fish and seal resources (Amorosi, 1992). The long occupation sequence seen at the site (the farm does not appear to have been abandoned until approximately 1888) also suggests that the occupants and their subsistence strategies were flexible enough to adapt to climatic change and survive. All of this evidence combines with the lack of change seen in the enamel hypoplasia record, to suggest that the occupants of Svalbarð and their flocks were far from being unwitting victims of climate change. Rather they appear to have successfully adapted and re-ordered their subsistence strategies to survive through the difficult times.

7.5.3 Seasonality

In Iceland, as in most northern temperate regions, lambing tends to occur in a tightly defined season. In Iceland this is slightly later than in Orkney (reflecting its more northerly location) meaning that the majority of births occur in May, along with the first growth of new grass (Bergthorsson, 1985). With this in mind, the enamel defects have been plotted against seasonal and physiological events. These are shown for the pre-1300 period in Figure 7.14 and for the post-1477 period in Figure 7.15.

The seasonal events have been slightly adjusted for climatic variation between the two figures. Sea ice is at its maximum extent in April and May and minimum levels in September to December (Ogilive, 1984). While sea ice has been plotted on both figures, it is important to remember that the effects of sea ice would have potentially been much more severe in the post-1477 period while in the pre-1300 period the effects would have been more limited. Eypórsson & Sigtryggosson (1971) define a normal ice year (as seen in the early 20th century) as one where the edge of the ice is 90-150 kilometres away from the northern coast of Iceland. In a severe year the ice can extend right along the northern coast of Iceland. Proximity of sea ice to the coastline causes both sea and land temperatures to fall (Eypórsson & Sigtryggosson, 1971). A systematic study into the effects of climate on Icelandic agriculture was carried out by Bergthorsson (1985). In this study, he demonstrated that the sea ice and variation in yearly temperatures had a profound impact on the annual grass yield, with cold winters causing dramatic falls in the grass yield. Sea ice plays an important role in the cooling effect of climate change providing negative feedback in its role as a heat sink, meaning that often one cold season would be followed by others (Ogilive & Jónsson 2001). In years when the sea ice was at its maximum extent, the growing season when the pastures renewed would have been shortened. This is reflected in the seasonal calendars created for the two periods at Svalbarð. The subsequent effect of this would have been that the fodder supplies for the overwintering of the animals

would have had to last longer, leading to fodder shortages as late in the season as May (Bergthorsson, 1985).

As seen in the previous populations studied from Orkney and Kenya, the various nutritional and physiological changes associated with birth are once again visible in both periods at Svalbarð as a peak of enamel hypoplasia in the mid regions of the first molar crown. In the pre-1300 population there is a second peak of enamel hypoplasia occurring on the first molar around 6 months after birth. This is again something seen in the previous populations studied and has been related to weaning. In the post-1477 population however, this 'weaning' peak is not visible at 6 months. Instead, in the post-1477 population following birth there is a near continuity in the frequency of enamel hypoplasia until approximately 5 months after birth (September) when the number of defects begins to decrease. This continuous high level of enamel hypoplasia in the post-1477 population immediately following birth is potentially related to the peak of mortality in young animals recorded in the faunal record, which Amorosi (1997) suggests is related to the increasing levels of sea ice and worsening climate associated with the Little Ice Age period.

The fact that weaning is not obvious in the Post-1477 population as a peak of enamel hypoplasia at 6 months after birth is intriguing. It possibly suggests that the animals were being weaned at a slightly earlier age in this population, accounting for the continuous high level of enamel defects until 5 months after birth.. As discussed in the previous chapters, forced weaning is not commonly practised excepted in modern intensive husbandry regimes, due to the pressures it places on the young animals. However, the reduced growing season suggested for the post-1477 population would have meant that by September grass supplies would be running low. The impacts of reduced fodder supplies on lactation are well documented in domestic caprines and discussed in the previous two chapters. It is therefore possible that decreasing fodder supplies at Svalbarð caused lactation to cease earlier in the post-1477 sheep forcing the weaning age earlier by a month.

In both second molars, a peak of enamel hypoplasia is visible in the cervical half of the crown. In the pre-1300 population this occurs around March / April. In the post-1477 population it occurs fractionally later around April / May. A very similar picture is seen in the third molars, with a clearly defined peak occurring in the pre-1300 population in May / June and a less obvious peak occurring in the post-1477 population at a similar time. Any differences seen between the two periods are subtle and therefore require cautious interpretation. The fact that both periods show very similar seasonal indicators of stress suggests that the changing climate had no radical impact on the lives and stress levels of the sheep flocks from Svalbarð. This supports the suggestion made earlier that the occupants of Svalbarð were adaptive in their approach to climate change and that by adjusting were able to maintain their animals general health levels throughout both periods.

The slight variation in the timing of enamel defects seen in the second molar (peaking around April in the pre-1300 population and fractionally later in the post-1477) is potentially explained by more extreme levels of sea ice delaying the early spring grass growth by a month or so. As mentioned above, this would lead to fodder supplies being stretched, resulting in extended periods of low nutrition. Bergthorsson (1985) suggests that one cold winter and spring could dramatically reduce grass growth and fodder supplies available to animals for subsequent year. When this is combined with the evidence from Ogilive & Jónsson (2001) who suggest that the negative feedback system caused by sea ice could lead to several successively cold years, it suggests that the animals at Svalbarð in the post-1477 period may well have suffered from extended periods of poorer nutrition in the early spring months. This is potentially visible in the enamel hypoplasia record as the slight increase in depression-type defects in the post-1477 period when compared to the pre-1300 period.

The third molar does not fit as comfortably with this hypothesis as the second molar. Peaks occurred in the third molar in both populations around the same time period (April / May / June) and the peak in the post-1477 population is not a clearly defined as in the pre-1477 population. As discussed in previous chapters the third molar's variable development rates and elongated growth periods are probably responsible, causing a wider degree of variation to be seen in the location of the enamel defects. This makes using the third molar to attempt to look at such a fine degree of resolution (1 month) difficult.

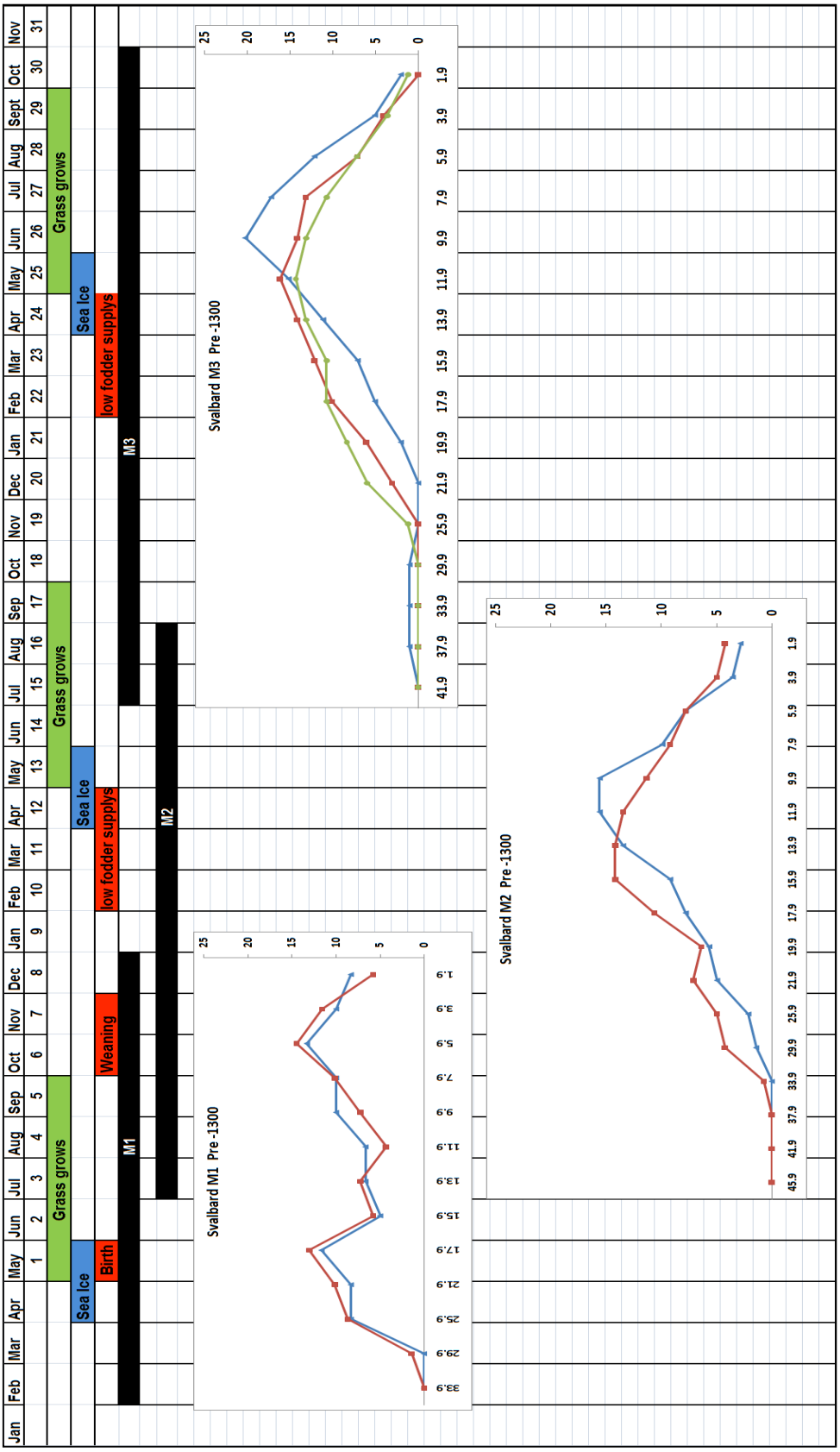

Figure 7.12: The data from Svalbarð pre-1300 plotted onto a chart of seasonal environmental and physical events. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.

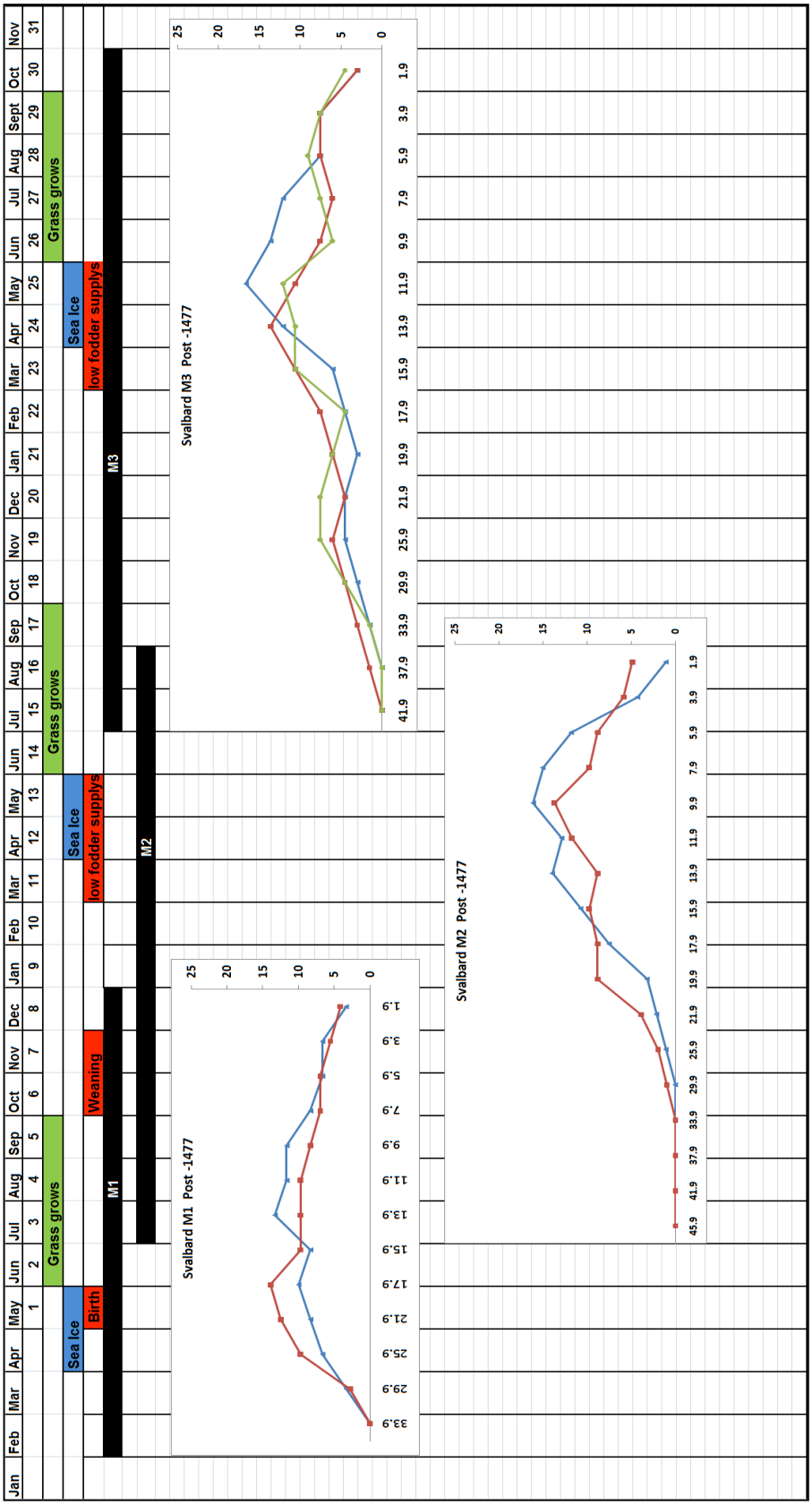

Figure 7.12: The data from Svalbarð post-1477 plotted onto a chart of seasonal environmental and physical events. Months after birth are marked along the top of the graph. The X axis shows the distance of the hypoplasia from the REJ, plotted up to the maximum tooth height in each molar (measured in mm). The Y axis shows the relative frequency of hypoplasia present.

7.6 Conclusions

7.6.1 General levels of population stress

Clear differences are seen between the sites of Svalbarð and Steinbogi in terms of both the numbers and types of defects present at each site. The higher frequency of depression-type defects seen at Svalbarð suggests seasonal periods of long mild stress as would be encountered during long cold winters with low fodder supplies. The very high frequency of linear-type defects seen at Steinbogi are likely linked to the changing management strategies present in the Mývatn region at this time, reflecting the intensification of sheep husbandry occurring in this region in the 13th and 14th centuries, leading to the intensive sheep farming models associated with the 18th century Jarðabók farms. The high number of linear defects (reflecting short, moderately severe stress events) may represent the associated pressures placed on pastures and fodder supplies, as well as various other factors associated with intensive husbandry regimes such as increased risks of parasitic and infectious diseases. The low economic status of the site, combined with the beginning of environmental degradation in the region, are also seen as compounding factors, adding additional stress to a probably already overstretched community.

7.6.2 Climate change

The lack of any caprine enamel hypoplasia data showing evidence linked to worsening climatic conditions of the Little Ice Age at Svalbarð post-1477 is intriguing. It combines with other evidence from the site, i.e. shifting subsistence strategies, increasing reliance on famine foods and marine resources, to suggest that the occupants of Svalbarð were in fact highly in tune with the changing environmental conditions and were able to adapt and re-organise their management

strategies accordingly to maintain the health and well-being of their livestock. The only evidence for a negative effect on the flock comes in the form of a mortality peak in neonatal lambs. It is suggested that if animals could survive this neonatal period then the occupants of the site had sufficient status, fodder supplies and management strategies in place to ensure the continued well being of their animals.

7.6.3 Seasonality

There are very few differences in patterns of enamel hypoplasia observed in sheep between the two periods at Svalbarð in terms of seasonality. Birth is visible in both populations as a peak of enamel defects in the middle of the first molar crown. Weaning is also visible at 6 months in the pre-1300 population. It is tentatively suggested that weaning may be occurring fractionally earlier in the post-1477 population due to decreasing grass availability in September causing the premature cessation of lactation. In the second molars slight variation in the timing of peaks in enamel hypoplasia are tentatively linked to shortened growing season in the post-1477 population, due to a cooler climate and the effects of sea ice. This would have lengthened the period where animals were reliant on fodder supplies which were potentially already stretched due to cooler climatic conditions. It is suggested that this led to increasing levels of malnutrition in the early spring months, possibly leading to the slight increase in depression-type defects in the post-1477 period.

7.6.4 Summary and future work

1) General levels of populations stress

Building on the work of the previous chapters, this chapter has applied the study of enamel hypoplasia to purely archaeological case studies. Using the frequency, type and severity of enamel defects as indicators of population stress, this chapter has

suggested possible explanations for the variation of enamel hypoplasia in terms of the economies and management strategies at the sites of Svalbarð and Steinbogi, in particular emphasising the introduction of a new, intensive, economic strategy in the Mývatn region combined with the beginnings of severe environmental degradation as a possible explanation for the high numbers of linear type enamel defects at Steinbogi.

2) Climate Change

A lack of change in enamel hypoplasia between the two climatic periods at Svalbarð, highlights the importance of contextual understanding when carrying out hypoplasia analysis. The lack of change in enamel hypoplasia combined with faunal and documentary evidence suggests that the occupants and their flocks were not as severely affected by climatic change as may have been previously assumed.

3) Seasonality

Again the physiological impact of birth and weaning are visible in the Svalbarð population, reinforcing the usefulness of hypoplasia analysis for looking at physiological events. Possible seasonal variation between climatic periods has been identified but the problems of resolutions especially in the third molar are highlighted.

4) Future work

A large scale study of the animal assemblages from the Mývatn district would enable a much more conclusive interpretation of the enamel hypoplasia from Steinbogi. The wide range of factors potentially affecting the animals from this site and the detailed environmental, social and archaeological work that has been carried out in the region make it an ideal target for a more detailed study of enamel defects. Allowing a more detailed assessment of the impact of status, environmental change and shifting animal management strategies on the animals, settlements and communities. Isotopic analysis of the Svalbarð population would also be of great interest, to investigate

possible variation in the climatic periods in terms of fodder provisioning. It would be expected, for example, that there would be an increasing reliance on seaweed in the post-1477 periods. This could be linked into a wider study of enamel hypoplasia with regard to fodder provisioning in the coastal and inland regions of Iceland.

8 Summary

This penultimate chapter draws together all of the data and results of the previous four chapters, to provide a critical analysis of the potential of enamel hypoplasia analysis in modern and archaeological caprine populations. This thesis has developed a methodology for the recording and analysis of enamel hypoplasia in caprines and applied it to three regional case studies, with very different environmental conditions. It has investigated multiple aspects of enamel hypoplasia in caprines around three principal research themes: 1) Methodological approaches to enamel hypoplasia in caprines 2) Understanding general stress levels, baseline causative factors and their implications in the interpretation of animal management and 3) Understanding seasonal and physiological impacts. Various aspects of each of these three main themes have been explored in the previous case study chapters, branching into areas such as the development of dental chronologies in caprines, the interpretation of defect types and the identification of animal management strategies. This chapter brings together all of the results, discoveries and conclusions made in these previous chapters.

8.1 Methodological approaches to recording and interpreting enamel hypoplasia in caprines

One of the major research aims of this thesis has been to develop a methodological approach to the study of enamel hypoplasia in caprines, which could resolve the many varied problems caused by high-crowned species. The method developed has been applied to modern and archaeological caprine populations in three geographical regions. This section aims to review the methodology created and to summarise the issues and problems faced in the application of this methodology to archaeological and modern caprine populations.

8.1.1 Is it possible to develop a methodological approach that will overcome the problems associated with high-crowned species and allow enamel hypoplasia to be recorded in caprine populations?

High-crowned species pose a variety of complex problems to both the recording and interpretation of enamel hypoplasia. Therefore, until recently, mainly low-crowned species (such as pigs, humans and great apes) have been the focus of studies into enamel hypoplasia (eg, Goodman & Rose, 1990; Moggi-Cecchi & Crovella, 1991; Dobney & Ervynck, 1998, 2000; Dobney, et al. 2002; 2004; Ervynck, et al. 2001; Guatelli-Steinberg, 2000; 2001; Franz-Odendaal 2004).

The methodology developed in this thesis is based on a combination of previous methodological approaches (in particular Dobney & Ervynck, 1998 and FDI, 1982), adjusted to make them suitable for use on caprine molars. The methodology involved recording enamel hypoplasia on the buccal surface of the permanent mandibular molars. The three key problems to the accurate recording and analyses of enamel hypoplasia in caprines are: coronal cementum, dental wear and tooth length. Research as part of this thesis has enabled all of these problems to be, if not 'solved'

then at least resolved, making the recording and analysis of caprine enamel hypoplasia viable.

Thin section analysis revealed that coronal cementum was present over all caprine molars, across all populations studied. Thin section analysis also demonstrated that, whilst coronal cementum was present over all teeth and enamel hypoplasia it rarely obscured enamel hypoplasia completely. The fact that it affected all populations meant that the only effect of coronal cementum was the consistent underscoring of enamel hypoplasia severity and the occasional complete obscuration of enamel hypoplasia. Therefore, while the problem of coronal cementum could not be wholly overcome, it was discovered that it was not a great hindrance or biasing factor in the recording of dental defects.

The fact that the majority of the tooth crown was obscured by the mandibular corpus was quite simply overcome by the extraction of the relevant molars. However, the problems of dental wear and tooth length were more complex. Detailed analyses of the effects of dental wear on the recording of enamel hypoplasia were carried out by investigating known age-at-death populations. This research revealed that enamel hypoplasia almost always occurs in the cervical portion of the tooth crown and that only a small percentage of the total tooth height was lost to dental wear in the four major Payne ages classes (C = 6-12 months; D = 1-2 years; E = 2-3 years and F = 3-4 years) studied in this thesis. Consequently as long as there was adequate representation of the younger age categories in each population studied to check for enamel hypoplasia in the upper portions of the teeth, there was little chance that recording teeth in more advanced wear stages would significantly bias the location of enamel hypoplasia to the lower half of the crown.

The second key problem posed by dental wear in caprine teeth was the fact that there are never complete unworn crowns available for study. This means that in complete molar crowns there is only ever the REJ available as a fixed reference point. This

makes it impossible to calculate the weekly growth rates of enamel, making it difficult to link the location of enamel hypoplasia to seasonal events. Dobney and Ervynck (1998) in their study of pig populations stated that if no complete teeth were present, animals with limited tooth wear could also be used to provide maximum height guesstimate measurements. Research in this thesis used a very similar method to deal with the potential problem of tooth wear. While there are never complete, unworn crowns available for study in caprine populations, there are complete crowns with very limited wear. After careful metric assessment to ensure there is no extreme variation in tooth size within the population, (inferring homogeneity), the height of the largest, complete, least worn crown from each molar group (M1, M2, M3), in each population was selected. This was then used as the baseline onto which dental defects were plotted. This baseline was then fixed against the developmental chronology for sheep teeth developed as part of this research. Complete teeth were selected with Payne (1973) wear stages of between 3 and 5 for use as baseline teeth, ensuring that only a few millimeters of tooth crown were missing. Once the teeth are fixed against the developmental chronology framework, the variation of a few millimetres of enamel becomes irrelevant, as it is broad time scale patterns that were being investigated and the rapid development rates of the occlusal half of the crown means that the occlusal section of the tooth represents only a very short time period.

The final problem dealt with in this research is one which potentially affects all population comparison studies using enamel hypoplasia: i.e. variation in tooth size between populations. Obviously, variation in the size of the tooth crown between populations can potentially seriously affect the relative chronology of enamel defects. This is especially true if larger teeth take longer to develop, as opposed to just developing faster. Using baseline teeth, plotted against a developmental chronology framework discussed above effectively deals with any associated problem of variation in tooth size between caprine populations.

How practical is this methodology?

Once teeth had been extracted they could be recorded by one person at a rate of approximately 100 teeth per day, allowing large amounts of information to be gathered in limited amounts of time. Unfortunately the process of tooth extraction from the mandibular corpus took much longer, with one person being able to extract the teeth from approximately 25 mandibles per day. The speed that this could be done was also highly variable depending on the preservation of the sample. For example modern material with a high collagen content took longer as the bone was less friable; whereas archaeological samples could often be extracted very quickly due to the fragile nature of the bone. The principal drawback to the methodology is the destructive nature of the extraction process, something which needs to be carefully considered for important archaeological assemblages. Whilst this destructive element can be removed, by focusing on isolated teeth, this also removes part of the analytical potential from the data, given the problem associated with separating isolated first and second caprine molars.

What problems are faced in recording the data using this method?

There are always problems associated with the implementation and repeatability of so-called systematic recording systems. The method developed as part of this research is no exception and two main problems were identified.

1) As observations were made with the naked eye it was possible that some defects were overlooked, particularly the more minor depression and linear type defects. The use of strong oblique lighting helped to over-come this problem, the use of a hand lens or retractable lens may also ensure that all defects are recorded, although the use of magnification was not adopted in this study.

2) It was occasionally difficult to verify the 'realness' of the most minor linear types of dental defects, given their sliding scale from the macro to the microscopic, and the problems of coronal cementum. Again the use of strong oblique lighting helped in the verification of enamel defects. If there was doubt, it was often found useful to re-record the tooth at a later date and check the defects originally recorded. It is worth noting here that re-recording was carried out on two occasions on the North Ronaldsay population in order to check the repeatability of the defect identification, and all the defects recorded in the original study were identified in the subsequent runs.

8.1.2 Can a developmental chronology for caprine teeth be created?

One of the biggest and perhaps most important challenges faced in the development of this methodology was the interpretation of the data collected. As such, the development of a reliable crown development chronology for caprines was essential if enamel hypoplasias were to be related to seasonal / physiological causes. A new developmental crown chronology was developed for use in this research from a known age-at-death population of modern sheep from Hoy (Orkney). Rates of enamel growth were investigated using thin section analysis, which revealed that the rate of enamel extension is not linear in caprine molars and therefore variation in enamel growth has to be accounted for when analysing the location of hypoplastic dental defects.

<u>What are the problems associated with the development of dental chronologies in caprines?</u>

The methodology developed has taken the first steps towards understanding the development rates of caprine teeth and enamel. However, there are clearly several areas in which this needs to be further developed. Problems and areas for future development relating to dental and enamel development chronologies can be summarised as follows:

- Resolution, while adequate for broad seasonal events, currently more detailed analysis of subtle changes in the timing of these events cannot be undertaken with complete confidence.
- Possible variation in the development rates in the third molar.
- Possible variation in the dental and enamel development rates between different sheep breeds

Clearly there is a need for more research to be undertaken concerning both the crown development rates and enamel deposition chronology of caprine teeth. Whilst the methods of data analysis developed in this research demonstrably appear to work, as peaks of hypoplasia can be correlated with expected physiological and seasonal events, the resolution obtained could be significantly improved. This would allow greater detail to be obtained on the timing of seasonal stress events. While the resolution has been adequate for many of the populations studied and even appears to be accurate to within a month in the Svalbarð population, a greater degree of resolution on the developmental rates of caprine tooth crowns and enamel would allow enamel hypoplasia to be correlated more confidently with the timing of physiological and seasonal stress events.

A more detailed chronology of the development of the third molar, combined with a more accurate assessment of the variation in development times of this tooth, would also enhance resolution in the study of seasonal stress events. It was noted in several of the populations (for example Svalbarð and North Ronaldsay) that peaks in the second molar regularly correlated with known or expected seasonal stress events but that in the third molar there was a less strong correlation. Often the peak of enamel hypoplasia in the third molar appeared to occur a month earlier or later than expected. It is suggested that this is due to a more varied rate of dental development in the third molar, potentially compounded by variation in dental development rates between caprine populations. It is suggested that more thin section analysis could

shed light on several of these issues, allowing a more detailed 'absolute chronology' to be ultimately created for dental and enamel development rates in caprine populations.

A more detailed investigation into the development rates of caprine teeth and enamel could then be integrated with research into the possible variation in dental development rates between breeds of sheep. The extent to which variation between caprine populations occurs is currently unknown. Therefore, its impact on the interpretation of enamel defects cannot be currently quantified. However, it is noted for the Kenyan populations used in this research that this is a potential source of error. The Kenyan populations are plotted against a dental chronology framework developed from Shetland sheep, a very different breed from a very different location. This fact possibly explains the slight lack of correlation between hypothesised seasonal drought periods and peaks of enamel hypoplasia in the Kenyan populations.

8.1.3 Are there any problems with the interpretation of the data using this methodology?

There were several difficulties faced in the interpretation of the enamel hypoplasia data which are summarised below:

1) Lack of enamel hypoplasia in the occlusal portions of the tooth crown.
2) Changing angles of the striae of Retzius and their impact on visible enamel defects.
3) Exact interpretation of defect types, particularly depression-type defects.

<u>Lack of enamel hypoplasia in the occlusal portions of the tooth</u>

It is important to note that the development periods of the first and second molars overlap by approximately 6 months and the second and third molars also overlap,

although only by around 2 months. Therefore, an overlap would be expected in peaks of hypoplasia, when they occurred in overlapping parts of the crown. In most cases however, this does not happen. When it does occur, for example in some of the Kenyan populations (particularly with regard to the weaning peak seen for example at Narosura, see Chapter 6 for details), the peak in the occlusal half of the tooth is never as large as the correlating peak on the cervical half of the previous tooth. This is almost certainly due to the early stages of amelogenesis, where the enamel is secreted in domes at the apex of the tooth, rendering the early incremental depositions invisible on the outer surface of the tooth. Also, the angle of the striae of Retzius with the cementum enamel junction becomes increasingly obtuse in the cervical portions of the crown, leading to the formation of apparently larger enamel hypoplasia (as discussed by Newell et al. 2006).

The impact of the striae of Retzius

This increasing angle between the striae of Retzius and the dentine enamel junction serves to also explain the occurrence of more severe hypoplasia in the cervical half of the tooth crown, as demonstrated in the North Ronaldsay population (discussed in Chapter 5). Tooth growth is slowest in the cervical half of the crown and the Retzius lines follow a less acute angle from the dentine to the tooth surface. This allows more minor hypoplasias to be more visible in this area of the tooth. Again, this needs further investigation using thin section analysis, particularly focussing on sections from teeth with overlapping development periods (such as the first and second molar) from the same individual. By studying overlapping segments of teeth, hypoplastic events could then be identified and correlated between the tooth crowns. This would allow a more detailed understanding of the development of the upper parts of the crown and reveal enamel hypoplasia that is not visible externally.

The interpretation of defect types

Defect types do appear to relate to variation in stress levels, with populations under higher assumed levels of stress showing increased frequencies of linear-type defects

compared to depression-type defects, something which is seen repeatedly in the caprine populations studied in this thesis. However, the data presented in Chapter 5 clearly demonstrates that further work is required, particularly with regard to depression-type defects and their relationship with the shift features seen in the North Ronaldsay population. This is an area that has been only briefly investigated in this thesis, as once it had been established that 'shift' type defects were not 'real' enamel hypoplasias then they were no longer recorded. However, given their apparently close relationship with depression-type defects this is clearly an area which needs to be investigated in more detail in both caprine and other high-crowned species. Thin section analysis in humans has clearly demonstrated a link between different types of enamel hypoplasia and different forms of stress events in humans (e.g. Witzel, et al. 2008, see discussion in Chapter 3). Similar research could be undertaken in caprines to help resolve some of the various interpretation issues regarding the types of hypoplasia and the forms of stress event which may have led to their production.

Other issues

Throughout the course of this research many problems have been raised and resolved, however, one potential issue has been raised by this research which has not been addressed, as it was not regarded as a potential complicating factor when the methodology was developed. The methodology focused on only the mandibular teeth and maxillary teeth were not included in this study due to the reasons outlined in Chapter 4. However, during the course of this research and collaboration with Dr M. Balasse and Dr A. Tresset (CNRS, Paris) it has been noted that when maxillary teeth are recorded for enamel hypoplasia they often contain a higher number of hypoplastic defects than mandibular teeth. This is clearly an area which requires more investigation, as hypothetically these teeth should reflect the same number of enamel hypoplasias, given that they are developing at the same time as the mandibular teeth. The fact that they display higher numbers of hypoplasia (noted now in three separate populations, Balasse pers. comm.) suggests that they are potentially more suitable for recording enamel hypoplasia, except for the various problems of aging and recording maxillary teeth that are discussed in Chapter 4.

Potentially the higher numbers of enamel hypoplasia noted in maxillary teeth relate to the internal structure of the teeth and the angle of the striae of Retzius, again this is an area which could be investigated using thin section analysis.

8.2 Understanding general stress levels, baseline causative factors and their implications of the interpretation of animal management

The second major research theme of this study has focused on developing an understanding of general stress levels, their causative factors and the implications of these baseline factors for the understanding and interpretation of animal management strategies within modern and archaeological caprine populations. This has focused on the use of enamel hypoplasia as a general indicator of population level stress, and investigated dietary, nutritional, climatic and environmental factors that cause 'stress' in caprine populations. This is the most basic level of interpretation of enamel hypoplasia data and therefore essential for understanding subsequent, more complex, interpretative methods.

8.2.1 Does enamel hypoplasia reflect 'general stress' at a population level in caprines?

As previously discussed, the use of enamel hypoplasia as a general stress indicator has been well documented in human populations (e.g. Sweeney, et al. 1966; 1969; 1971; Goodman, et al. 1980; Wood, et al. 1992; Oyamada, et al. 2008; see Chapter 3 for detailed overview). Consequently it was the first thing to be investigated in caprine populations. Obviously it was expected that populations under greater levels of general stress (environmental / climatic / nutritional / physiological) would reflect this in the frequency of enamel hypoplasias recorded. General levels of population stress and their relationship to the frequency and severity of enamel hypoplasia were tested using the two modern populations from Orkney (Hoy and North Ronaldsay, discussed in Chapter 5). These two modern populations from Orkney were similar in many ways: both were primitive breeds, living in the same geographic area and subject to 'unmanaged' husbandry regimes. However, in terms of lifestyle, the animals from North Ronaldsay were under considerably more stress than those from

Hoy. They live in considerably more challenging environmental conditions, penned all year around on the beach with an unusual diet of seaweed, to which they are potentially not as well adapted as previously thought (Britt & Baker, 1990; see discussion in Chapter 5). The frequency and severity of the enamel defects were compared between the two populations and the increased level of 'general stress' in the North Ronaldsay population was clearly visible. The North Ronaldsay population showed a significantly higher frequency and severity of enamel hypoplasia when compared to the population from Hoy. This preliminary study clearly demonstrated the use of enamel hypoplasia as an indicator of 'general stress' levels in caprine populations.

8.2.2 What are the baseline factors that affect enamel hypoplasia in caprine populations?

Enamel hypoplasia in humans is seen as an indicator of 'general stress' therefore there are multiple factors that can lead to its formation (Goodman and Rose, 1990; Dobney and Goodman, 1991; Kierdorf, et al. 2004 and Witzel, et al. 2006). Once it had been identified that enamel hypoplasia could be used to identify caprine populations facing greater levels of 'general stress' a more detailed investigation into underlying factors was possible. Within all populations there are consistent factors (such as nutrition level; discussed in chapter 3) which need to be maintained to ensure the population's health. It is when 'thresholds' in health status are crossed that variation occurs in the frequency of enamel hypoplasia. It was felt important to briefly investigate these baseline factors, as it is variation in the expression of enamel hypoplasia between populations with similar baseline factors that will allow secondary impacting factors, such as animal management strategies to be interpreted. Therefore this research identified two closely interlinked factors which were assumed to be active in the formation of enamel defects in all caprine populations. These were the local environment / climate and the diet or available nutrition levels of the population.

Does climatic and environmental variation impact upon enamel hypoplasia formation in caprines?

The environment and climate clearly play a vital role in any assessment of 'general health' within a population. Changes in environmental / climatic conditions lead to a variety of potential stressors, including periods of malnutrition and extreme weather for example, extreme cold and drought. A specific study into the impact of environmental variation was carried out in the analysis of the modern Kenyan population (published by Balasse, et al. In press and summarised in Chapter 6; see also Appendix 1). In this study, two populations comprising the same breeds and managed under identical husbandry regimes were compared; the first from a semi arid region and the second from a more mesic region of Kenya. As expected the animals from the more mesic region displayed higher frequencies of enamel defects. While this comparison is basic, it clearly demonstrates that environmental conditions are an important underlying factor in the formation of enamel hypoplasia in caprine populations.

Does nutrition impact on enamel hypoplasia formation in caprines?

Nutrition and its direct impact on the formation of enamel hypoplasia, is very difficult to separate from the impact of environmental variation. Indeed it is argued in Chapter 6 that the differences seen between the two regions of Kenya discussed above are due to the more limited availability of food resources during drought periods in the arid region than in the more mesic region. The impact of nutrition is clearly highlighted in the comparison of sheep and goat from the same environmental region in Kenya (Balasse, et al. In press; discussed in Chapter 6). Sheep were found to have higher frequencies of hypoplasia as well as more severe linear defects than goats. It was suggested that this was due to the different dietary preferences favoured by the two species. Goats are browsers whereas sheep are grazers, therefore goats are better at utilizing available food resources in periods of drought when resources are scarce. Again this is a basic comparison but one which clearly demonstrated the

important role of nutrition and the availability of food resources as an underlying factor in the formation of enamel hypoplasia in caprines.

8.2.3 Can variation or change in animal management strategies be seen in the enamel hypoplasia of caprine populations?

Having established that enamel hypoplasia could be used as a general indicator of population stress, and that the local environment / climate and available food resources were baseline factors in the formation and severity of enamel hypoplasia, it was important to investigate if variation in the frequency severity and type of enamel defects could be utilised to investigate archaeological questions regarding animal management practises. Animal management strategies have been identified in the previous three chapters in several ways: Firstly, variation in animal management between populations has been identified by comparing populations with identical baseline factors and identifying differences in the frequency, severity, type and location of the enamel hypoplasia. This was observed in the comparison of modern and archaeological material from Orkney in Chapter 5 and in the archaeological populations from Kenya, discussed in Chapter 6. Differences in animal management strategies can be identified in these populations because the baseline factors are known to have been the same, or can be assumed to be the same, given the close environmental proximity of the sites. Therefore, variation in enamel hypoplasia cannot be seen as representing variation in the baseline factors and can be tentatively interpreted with the aid of contextual information as variation in animal management. The second interpretation of animal management is almost the reverse of the first approach and occurs when known climatic / environmental variation has been identified in a region but is not visible in enamel hypoplasia record. This is purported for the modern Kenyan material discussed in Chapter 6 and archaeological material from Iceland discussed in Chapter 7.

How can enamel hypoplasia be used to identify animal husbandry practises?

One of the most interesting examples of the use of enamel hypoplasia for investigating animal management strategies comes from the comparison of the two modern Orkney populations to the archaeological populations from Skara Brae. The significantly lower number of enamel defects seen in the Skara Brae population, when compared to the two modern populations, is striking. Both modern populations exist largely unmanaged, leading to seasonal periods of malnutrition and the marginal Orcadian climate impacting upon their health, causing high numbers of enamel hypoplasia. The low number of defects recorded in the Skara Brae caprine population contrasts wholly with these modern baseline assemblages. It suggests that many of the stressors operating in the modern populations were not present in the Neolithic, potentially indicating a carefully managed animal population or perhaps milder seasonal impacts upon the ancient sheep population. The pattern from Skara Brae would fit with a small number of animals being kept in carefully managed flocks. This small, household-scale animal husbandry would have allowed the occupants of Skara Brae to ensure the health and wellbeing of those flocks throughout the seasonal periods of poor weather and low fodder supplies. Variation between the Neolithic and the modern day climate / vegetation is also considered as a possible explanation for the increase in enamel defects in modern populations. It is suggested that the cooler, damper modern climate and the reduction in available fodder due to blanket peat formation, places increased pressure on seasonal fodder supplies in the modern populations.

The study of the Orkney caprines has also hinted at the potential to use these defects to indicate ancient foddering practises. The low frequency of enamel hypoplasia seen in the Skara Brae population is also seen in two other Neolithic populations from Orkney (Knap of Howar and Holm of Papa Westray). Isotopic analysis of these two populations indicated that the population with the lowest frequency of enamel hypoplasia were eating a mixture of seaweed and grass, while the animals with higher frequencies were eating only grass (Balasse, et al. 2006). The frequency values for enamel hypoplasia seen at Skara Brae were intermediate to those observed

at the other sites. This suggests that animals at Skara Brae may have also had their diets supplemented with seaweed. This begins to hint at the possibility of using enamel hypoplasia as an indicator of diet and foddering practises, although admittedly with careful analysis of contextual information and other supporting lines of evidence, such as regional palaeoenviromental and isotopic data.

The caprine enamel hypoplasia evidence from Kenya indicated that the animal management strategies of the two different archaeological cultures (Elmenteitan and Savannah Pastoral Neolithic) were broadly similar, with no clear differences appearing between the two cultural groups in terms of the frequency, type or severity of enamel hypoplasia. This was to be expected given the groups apparently similar form of specialised pastorialism. However, the results did show some clear differences between the different types of the site studied (rock-shelters versus open plain), with the small rock shelter assemblage from Enkapune Ya Muto showing considerably higher frequencies of enamel hypoplasia than the open plain sites. This rock shelter site was also interesting because of the unusually high frequency of enamel hypoplasias seen in the goat population compared to sheep. It was demonstrated in the modern material that goats suffered less stress than sheep due to their utilisation of wide variety of food resources in drought periods (Balasse, et al. In press). However, this was clearly not the case at the site of Enkapune Ya Muto. This information, combined with the archaeological evidence suggesting variation in the uses of the two different types of site, indicated that something very different was happening at this site in terms of caprine management strategies. The modern evidence clearly indicates that if the animals are herded together, sheep will manifest signs of physiological stress through enamel hypoplasia more readily than goats - the opposite of what was observed at Enkapune Ya Muto - suggesting that the caprines were being herded separately. Supported by associated isotopic and archaeological evidence (Balasse & Ambrose 2005a) the goats were very likely to have been either penned in the rock shelter or kept in the vicinity of the site, while sheep were herded both around the site and down onto the valley floor.

Animal management strategies can clearly be identified in comparisons between sites which share similar environmental / nutritional levels. However, animal management strategies have also been identified where there is a lack of variation in enamel hypoplasia data within populations where the base levels of nutrition / environment are known to have dramatically altered. This is clearly seen in the modern caprine population from Kenya which was assessed for the impact of the severe drought that occurred in 2000 (Balasse, et al. in press; discussed in Chapter 6). It is also identified in the archaeological population from the Icelandic site of Svalbarð, which was specifically investigated to explore the impact of the Little Ice Age (discussed in Chapter 7) on caprine health and management.

It was expected that the severe drought that impacted on the modern Kenyan populations in the year 2000, and the increasingly unstable climatic conditions associated with the onset of the little Ice Age in post-1477 Iceland, would be observed as increasing frequency and severity of enamel hypoplasias in these populations. This was assumed because these dramatic climatic / environmental changes should significantly alter the baseline factors (outlined above) in the formation of enamel hypoplasia, lowering the thresholds at which enamel hypoplasia would form. However, an increase in enamel hypoplasia frequency and / or severity could not be identified in association with either of these severe climatic events.

There are several possible explanations for the lack of visibility in the data of these two dramatic climatic events. It must be remembered that the formation of enamel hypoplasia indicates survival. Potentially these climatic / environmental impacts were so severe that animals died before these events could be recorded in their dental enamel. Alternatively it suggests a degree of flexibility and resilience within the animal management strategies themselves, to compensate for such climatic variation. For example it is known that within the modern Maasi there are close family and intra family alliances that allow animals to be moved over long distances to available water sources during drought periods (Balasse, et al. In press). For the archaeological population from Svalbarð in Iceland, it perhaps indicates that the occupants of the

site were not just unwitting victims of climate change. It implies that they were, in fact, flexible and adaptive in their approach to animal management and, as such, were able to protect and buffer their caprine flocks from the impact of the increasingly unpredictable and poor climate.

8.3 Understanding seasonal and physiological impacts in caprines

The final area of this research has focused on developing more complex interpretations of enamel hypoplasia, specifically linking its formation to known seasonal or physiological events. This has been one of the more complex (and perhaps still tentative) elements of this research, requiring detailed investigation into the development rates of caprine teeth and dental enamel. However, this form of analysis can potentially provide detailed information on the occurrence of seasonal stressors and their impact on caprine flocks, the potential of which has at least been demonstrated by the data observed in this thesis.

8.3.1 Are specific physiological stress events visible in the enamel hypoplasia record for caprine populations?

Physiological events such as birth and weaning have been identified in both archaeological, modern, animal and human populations as a cause of enamel hypoplasia (e.g. Sarnat and Schour, 1941; 1942; Corruccini, et al. 1985; Goodman, et al. 1987; Whittaker & Richards, 1978; Dobney & Ervynck, 2000; see chapter 3 for a detailed discussion). Physiological events cover a range of potential causes of stress. However, the physiological stress events most commonly identified by enamel hypoplasia during this research on caprines were birth and weaning. A range of other factors such as gestation, lactation, seasonal cycles of parasitic infection and fodder shortages could potentially also be observed in later peaks of dental defects.

<u>Is the nutritional and physiological stress of birth visible in the enamel hypoplasia record?</u>

Birth is well documented in both humans and animals as a cause of enamel hypoplasia (e.g. Sarnat and Schour, 1941; 1942; Dobney & Ervynck, 2000). It

produces a variety of stresses, including the physical trauma of birth, a dramatic environmental change and often a period of malnutrition as the neonate adjusts to a new diet. By plotting enamel hypoplasia against a chronological framework of crown development, enamel hypoplasia linked to the trauma of birth has been identified in several of the caprine populations studied (primarily Orkney and Iceland). The fact that birth is not apparently recorded in the enamel of all of the caprine populations studied is of course interesting. Birth in caprines is not necessarily as stressful as in other animal populations as birth in ungulates is usually a quick process, necessitated by the vulnerability of the mother and the young to predation. This, combined with the fact that birth is not visible in all of the populations studied, suggests that it is not the actual physical stress of birth in caprines that causes enamel hypoplasia but rather the immediate surrounding environment. Given that the animals obtain nutrition from their mothers for the first few months of life, environmental factors such as drought leading to low fodder supplies are less likely to cause stress at birth. However, extremely cold climates would be stressful as they would directly impact on the neonatal animals. The fatal effect of cold weather on neonatal lambs for example is well documented (Portier, et al. 2000). When the populations from all three geographic regions are compared, the stress of birth is most obvious at the Icelandic site of Svalbarð, with high percentages of first molars displaying enamel hypoplasia correlating with birth (Figure 8.1). The second highest correlation of enamel hypoplasia with birth is then seen in the North Ronaldsay population from Orkney. It is harder to assess the impact of birth in the Hoy population from Orkney, given the low numbers of defects recorded on the first molar. There is almost no enamel hypoplasia correlating with birth in any of the modern or archaeological Kenyan populations studied. This clearly suggests that birth, whilst visible in the enamel hypoplasia record in caprine populations, is more likely to be visible in populations which have climatic / environmental conditions likely to directly impact on the health of neonatal animals.

Is the nutritional and physiological stress of weaning visible in the enamel hypoplasia record?

Weaning unlike birth, directly impacts upon the nutritional levels of all young animals, regardless of their environmental surroundings. The impact of weaning on enamel development was identified in all of the populations studied, in the form of peaks of enamel hypoplasia occurring most commonly around 6 months after birth on the cervical half of the first molar (Figure 8.1). However, in the Kenyan populations, weaning also appears to be visible on the second molar, with a small peak of defects occurring in the occlusal half of the 2nd molar (see Figure 8.2). This is most clearly seen in the archaeological population of Narosura, Kenya. It is unclear why observations of enamel hypoplasias linked to weaning are present on the second molars in some populations and not in others. As discussed above in section 8.1.3 it is most likely related to the internal structure of the tooth, which causes enamel hypoplasia in the occlusal portion of the tooth crown to be less visible.

The appearance of a peak in enamel hypoplasia around 6 months after birth related to weaning was expected. This fits with the pattern of natural unforced weaning that is likely to have occurred in all these populations. In natural weaning, complete separation has occurred between the mother and her offspring by approximately 8 months after birth, making the proceeding months nutritionally challenging as the young animal is slowly forced to adapt to its new diet. There was some slight variation seen in this pattern of natural weaning between the populations studied, probably of most interest with regard to the Icelandic population of Svalbarð where in the post-1477 period, weaning appears to be occurring fractionally earlier, with an extended peak of enamel hypoplasia running from birth to around 5 months of age. It is suggested that the worsening climate seen in this period led to reduced grazing availability in September causing early cessation of lactation in this population, forcing the onset of earlier weaning at around 5 months of age.

Are any other physiological stress events such as gestation and lactation identifiable in the enamel hypoplasia record?

There are of course numerous other physiological stressors which could potentially cause the formation of enamel hypoplasias in caprine populations, primarily: gestation and lactation in females; and castration and competition for mates in males. However, none of these other physiological factors have been identified in the enamel hypoplasia record of any of the populations studied This may be due to peaks in baseline stressors masking peaks caused by other factors. This is potentially an area which could be investigated further using modern populations with more specific information available.

Other physiological stressors which can impact upon the formation of enamel hypoplasia include infectious / parasitic diseases and trauma. All are an obvious cause of physiological stress and almost certainly can lead to the formation of enamel defects as clearly demonstrated in experimental work carried out on sheep teeth (see detailed discussion in Chapter 3). However, it has been demonstrated that these stressors are overshadowed by the key baseline factors discussed previously. The impact of infectious or parasitic conditions for example, will have a more severe impact on the formation of dental enamel if the population is malnourished or under extreme environmental / climatic pressure and therefore these underlying factors are the ones which are repeatedly most visible in the enamel hypoplasia record. Clearly this has potential as an area of future investigation, through the analysis of populations which have undergone known and identifiable periods of parasitic or infectious disease and correlating these to enamel hypoplasia formation and severity.

8.3.2 Are seasonal stress events visible in the enamel hypoplasia record?

The investigation of seasonal stress events and their visibility in the enamel hypoplasia record has been one of the most interesting and informative elements of this research in caprines. In the previous three chapters, peaks in enamel hypoplasia have been correlated with detailed seasonal data frameworks and have produced a

wide range of interpretable results (see Figure 8.2 & Figure 8.3). In Chapter 5 a comparison was made between two modern populations from Orkney with known differences in their seasonal periods of stress. Comparisons between the seaweed-eating sheep of North Ronaldsay and the grass-eating sheep of Hoy provided the first clear evidence that seasonal periods of malnutrition could be identified in the enamel hypoplasia record. Clear variation in the location of the peaks of enamel hypoplasia in the second and third molars between these two populations correlated exactly with the different periods of nutritional stress that affected each population. The North Ronaldsay population suffered their greatest period of nutritional stress during the summer months, while the Hoy population would have been in peak condition, given the large amount of available grass during the early summer at least. In the winter months, the North Ronaldsay population was at their nutritional peak as winter storms washed large quantities of nutritionally rich seaweed onto the beach. The Hoy population by comparison in late winter/early spring were reaching a nutritional low as winter grass and fodder supplies ran low.

Chapter 6 extended the analysis of seasonal events one stage further and attempted to reconstruct seasonal periods of stress events in archaeological populations. This was aided by a re-analysis of the modern Kenyan material with its known seasonal factors as a baseline for comparisons. Given the similarities in enamel hypoplasia patterns between the modern material and the archaeological populations studied, it is suggested that seasonal stressors may have been very similar in the Kenyan Neolithic as they are in modern Kenyan populations. Based on this, and the environmental and archaeological evidence for a bimodal rainfall pattern in the Neolithic, both populations were plotted against a calendar of likely seasonal drought periods. Although, there are some potential problems with this hypothesis (discussed in detail in Chapter 6), there appears to be a positive correlation between increases in enamel hypoplasia and seasonal periods of drought in both the modern and the archaeological populations. This supports the association outlined in previous sections that malnutrition and environmental / climatic variation play a key role in the formation, frequency and severity of enamel hypoplasia.

In Chapter 7 the investigation of seasonal defects was carried out on a purely archaeological population. The site of Svalbarð on the northeast coast of Iceland is known to have suffered from the increasing poor environmental conditions associated with the climatic cooling event known as The Little Ice Age. The caprine sample was divided into two data sets to be compared: the pre-1300 (Medieval Warm period) and the post-1477 (The Little Ice Age period). Similar seasonal stressors were hypothesised for both populations - primarily the occurrence of sea ice in the early spring, coinciding with the exhaustion of winter fodder supplies and harsh winter weather. However, for the post-1477 population the timing of these events are assumed to have been extended into the late spring due to the increasing presence and proximity of sea ice documented in these periods. When the enamel hypoplasias are plotted against the seasonal calendars, there is a clear correlation between the purported period of malnutrition and sea ice in both populations. Also the suggested extension (due to the proximity of sea ice) of these early spring stressors into the later spring months in the post-1477 population is also argued to be visible. The peak of defects on the second molar clearly extends into May and July in the post-1477 population but ends in April in the pre-1300 population.

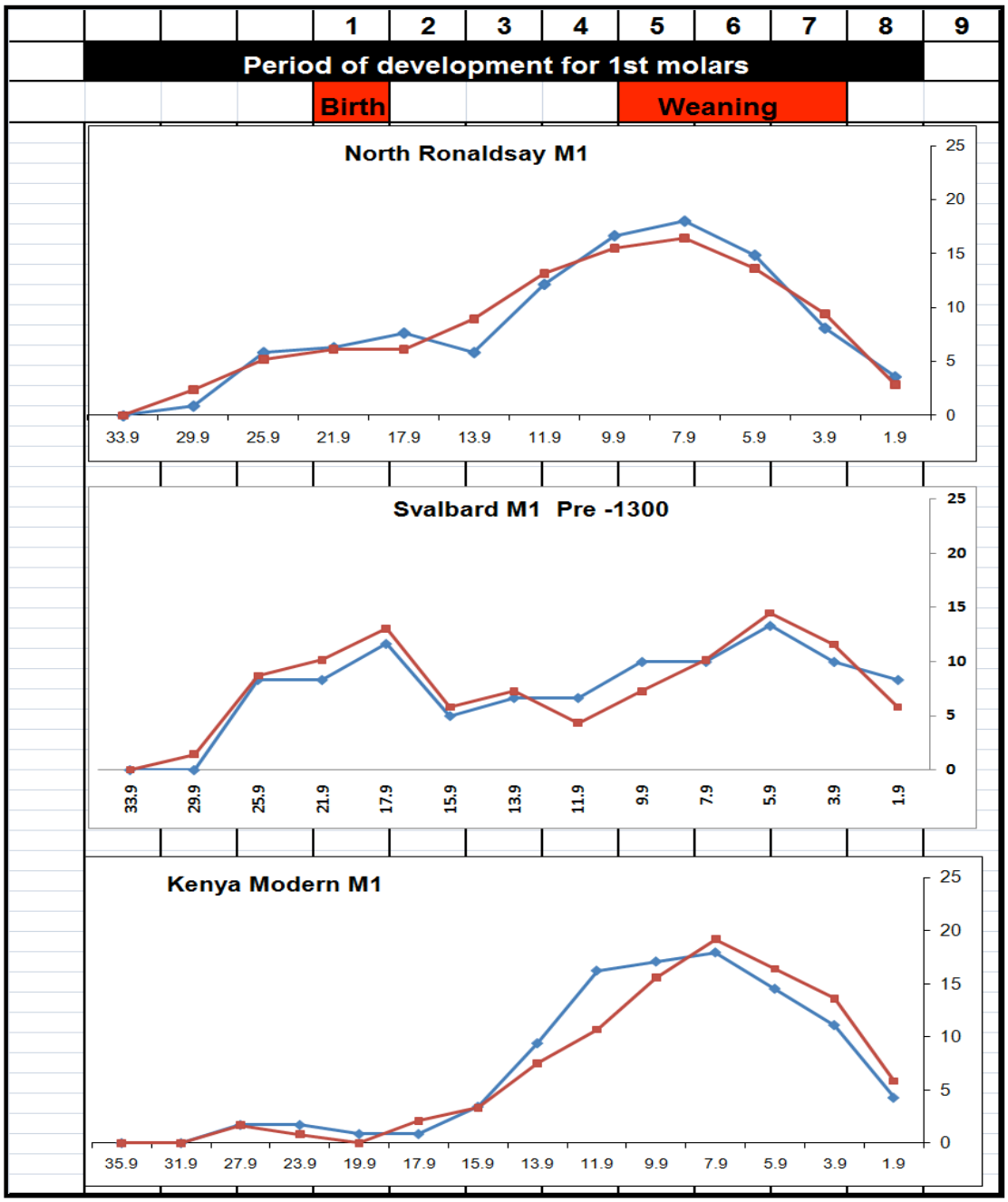

Figure 8.1: Comparison of the distribution of enamel hypoplasia on the 1st molar across 3 populations. Months after birth are numbered across the top of the graph. The X axis represents the relative frequency of hypoplasia present. The Y Axis shows the location of hypoplasia on the tooth crown (mm). Birth is clearly most visible in the Icelandic population of Svalbarð and not visible at all in the Kenyan population. Peaks relating to weaning occur in all 3 populations between 5 and 7 months.

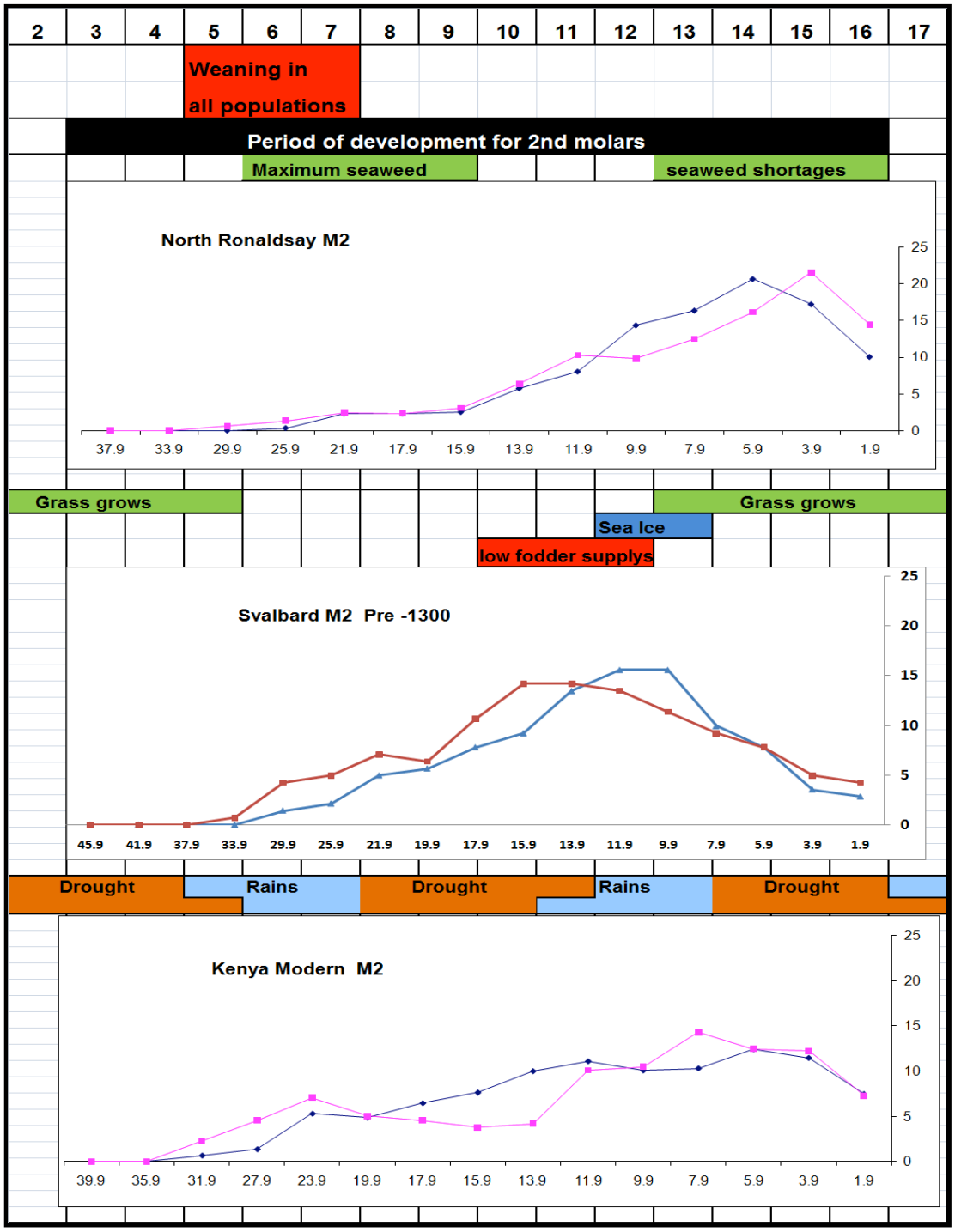

Figure 8.2: Comparison of the distribution of enamel hypoplasia on the 2nd molar across 3 populations. Months after birth are numbered across the top of the graph. The X axis represents the relative frequency of hypoplasia present. The Y Axis shows the location of hypoplasia on the tooth crown (mm). Population specific factors affecting the development of enamel hypoplasia in each population are shown above each graph.

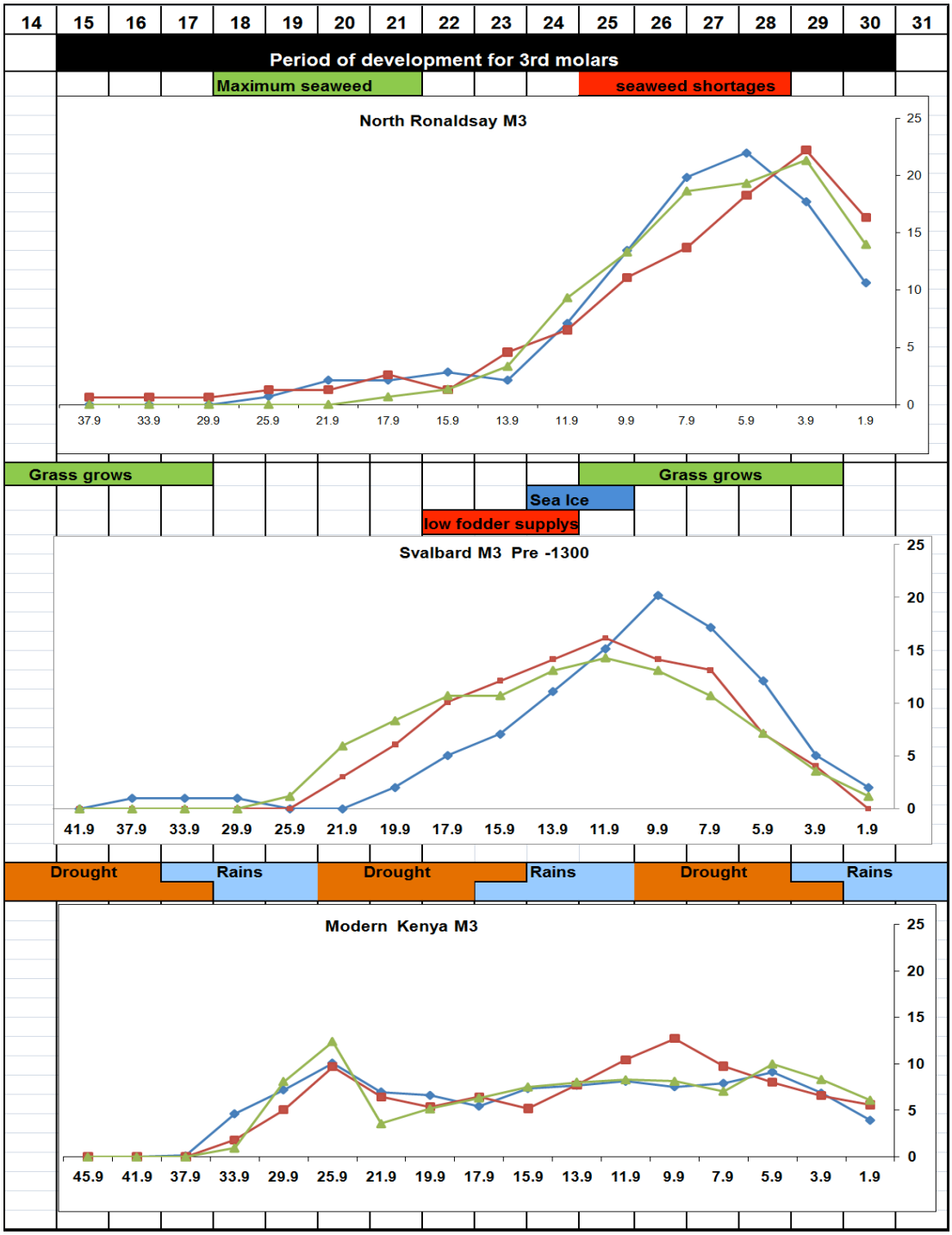

Figure 8.3: Comparison of the distribution of enamel hypoplasia on the 3rd molar across 3 populations. Months after birth are numbered across the top of the graph. The X axis represents the relative frequency of hypoplasia present. The Y Axis shows the location of hypoplasia on the tooth crown (mm). Population specific factors affecting the development of enamel hypoplasia in each population are shown above each graph.

9 Conclusions

This final chapter outlines briefly the principal conclusions drawn relating to each of the major research themes and key questions that have been addressed in this thesis and suggestions for future work are outlined for each.

9.1 Methodological approaches

This first research theme has focused on the development of a methodology to allow enamel hypoplasia to be recorded in modern and archaeological caprine populations. It has critically explored issues relating to recording, analysis and interpretation of enamel hypoplasias in caprines as well as the development of dental chronologies for caprine molars.

9.1.1 Is it possible to develop a methodological approach that will overcome the problems associated with high-crowned species and allow enamel hypoplasia to be recorded in caprine populations?

This research has successfully created and applied a methodology for recording and analysing enamel hypoplasia in animals with high-crowned teeth – in this case caprines. There are still minor methodological problems associated with the approach, but it has been demonstrated that enamel defects can be relatively quickly and systematically recorded in both modern and archaeological populations, and that meaningful datasets can be generated.

9.1.2 Can a developmental chronology for caprine teeth be created?

The development of a chronology of dental development and enamel growth has been one of the most challenging aspects of this research. There are still a variety of potential problems with the chronology that has been formulated; however, it is felt that with ongoing thin section analysis of modern caprine populations these will eventually be resolved. The basic dental chronology created for use within this research has successfully correlated enamel defects with specific season / physiological events, although the resolution could of course be improved.

9.1.3 Are there any problems with the interpretation of the data using this methodology?

There are various problems associated with the analysis of enamel hypoplasias in caprine populations, including the complex internal structure of high-crowned teeth and the relationship of defect types with different forms of stressors. However, it has been demonstrated in this thesis that none of these jeopardise the accuracy of results obtained.

9.1.4 Summary and future work

Whilst there remain many unresolved questions regarding the internal structure and development rates of caprine teeth, the basic method created for recording and analysing enamel hypoplasia in caprine populations has been placed upon a demonstrably sound footing. Teeth, once extracted, can be recorded easily and quickly, with the only negative aspect being the minor destruction that comes with extracting the teeth from the mandible. When enamel hypoplasias are compared with notional seasonal and physiological calendars there is a clear correlation between expected stress events and peaks of enamel hypoplasia, demonstrating, that the recording methodology and dental chronology created for data analysis in caprines are at least viable. Indeed in Icelandic material, the method of analysing the data within dental chronologies even appears to be accurate to the month, as demonstrated

in the minor shift in defects correlating with the purported extension of the seasonal periods of stress relating to sea ice proximity.

Clearly there is scope for future research to be undertaken refining this methodology in terms of the creation of more detailed and comprehensive dental chronologies. This would allow for a higher degree of resolution to be obtained from the analysis of hypoplasia and may allow for more subtle changes in seasonality to be positively identified. Thin section analysis could go a long way to answering many of the interpretative questions raised by this analysis, particularly with regard to the internal structure of the teeth and its impact on enamel hypoplasia in the upper regions of the tooth crown. One of the key aspects for future work is the continued investigation into the relationship between defect types and stress events. Particularly with regard to the depression-type defects and their apparent correlation with shift anomalies.

9.2 Understanding general stress levels, baseline causative factors and their implications of the interpretation of animal management

The second principal research theme has been based upon developing an understanding of stress at a population level as well as investigating the causes of stress and their implications for the interpretation of animal management strategies.

9.2.1 Does enamel hypoplasia reflect 'general stress' at a population level in caprines?

Clearly enamel hypoplasia can be used as an effective measure of 'general stress' in caprine populations. This research has repeatedly demonstrated that populations facing greater levels of general stress in the form of difficult environmental / nutritional / climatic / physiological conditions display higher frequency and increased severity of dental enamel hypoplasia.

9.2.2 What are the baseline factors that affect enamel hypoplasia in caprine populations?

As enamel hypoplasia is commonly seen as a general indicator of stress the identification of specific factors has been difficult. The inter-linking relationship between climate / environment and nutrition is suggested as a key factor in all caprine populations. Variations in these factors have been repeatedly demonstrated to impact on the frequency, severity and type of enamel hypoplasia recorded.

9.2.3 Can variation or change in animal management strategies be seen in the enamel hypoplasia of caprine populations?

This research has demonstrated that enamel hypoplasia can be used in several ways to investigate caprine management strategies in archaeological populations. However, it is also clear that, given the wide range of causative factors, enamel defects need to be very carefully interpreted. It is vital that enamel hypoplasia is interpreted in the context of the baseline factors of environment /climate and nutrition, as well as archaeological contexts such as palaeoclimatic data. When used in these detailed contexts, enamel hypoplasia has been demonstrated to be a powerful tool for investigating variation in animal management regimes between populations. However, this research has also demonstrated that without the necessary contextual information the use of enamel hypoplasia can be limited and speculative.

9.2.4 Summary and future work

Enamel hypoplasia has clearly been demonstrated to relate to increased levels of 'general stress' in populations. The baseline factors of environmental / climatic variation are closely linked with the factor of malnutrition and the combination of these elements affect the formation and severity of enamel hypoplasia in all of the caprine populations studied. Variation in enamel hypoplasia from populations with similar baseline factors has then been used to identify possible variation in animal management strategies. Conversely, a lack of variation in enamel hypoplasia, where there is known variation in these baseline factors has also been used to identify animal management strategies.

Future work is outlined at the end of each of the previous three chapters with regard to the specific populations studied. However in general terms the further investigation into the causative aspects of enamel hypoplasia in caprines is vital. Whilst enamel hypoplasia is regarded as a 'general stress' indicator, this work has clearly demonstrated that it can be linked to quite specific baseline causes. More

work on modern populations with known life histories would clearly enhance our understanding of the exact impact of these complex and often interlocking baselines.

9.3 Understanding seasonal and physiological impacts in caprines

This research theme has focused around the investigation of physiological and seasonal stress events in caprine populations. This research has been based on the hypothesis that physiological and seasonal stressors can be related to peaks in enamel hypoplasia prevalence. This aspect of research has been conducted using primarily modern populations with known seasonal events acting upon them. This has then been developed to include application on archaeological populations.

9.3.1 Are physiological stress events visible in the enamel hypoplasia record for caprine populations?

Birth has been demonstrated as a cause of enamel hypoplasia in several of the populations studied and the visibility of this event has been correlated to the local climatic / environmental conditions into which the animal is born. The fact that birth is not visible in all of the populations is related to the fact that birth in ungulates is not normally considered to be a stressful process in itself, but rather the stress is caused by the adaption to a dramatically different environment and the slight period of correlating malnutrition. This research suggests that the adaption to cold climatic conditions increases this birthing stress in neonates, making it more visible in the North Atlantic populations studied than populations from the hot and arid regions of Kenya.

Weaning is visible in all of the populations studied. The ability to recognise weaning in both modern and archaeological populations highlights the potential for enamel hypoplasia to be used to investigate animal management strategies (e.g. enforced weaning). It has been tentatively suggested that earlier weaning occurred in one of the Icelandic populations studied in relation to low fodder supplies causing the premature cessation of lactation.

It is suggested that other physiological events may also be visible in the enamel hypoplasia record, such as seasonal cycles of parasitic / infections disease and gestation / lactation, but that more specific population based studies are required to investigate this further.

9.3.2 Are seasonal stress events visible in the enamel hypoplasia record?

Seasonal periods of stress have also been clearly identified in this study where enamel hypoplasia has been plotted against dental development chronologies and against seasonal calendars. These have revealed that the underlying baseline factors of climate / environmental change and associated malnutrition, appear to have the most significant impact on the occurrence of enamel hypoplasia. By plotting enamel hypoplasia in this way, a variety of seasonal stressors have been identified, including; 1) periods of drought in Kenya caused by the bimodal rainfall patterns; 2) periods of malnutrition in Orkney relating to the availability of food resources; and 3) the early spring fodder shortages (and their extension into the late spring) in the post-1477 period of the Little Ice Age in Iceland.

9.3.3 Summary and future work

When used in conjunction with adequate comparative, environmental and archaeological data, enamel hypoplasia is potentially a powerful tool for investigating archaeological questions regarding variation in animal management strategies between sites, environmental / climatic variations and periods of seasonal and physiological stress affecting caprines. It has been demonstrated that there is a clear correlation between seasonal and physiological stressors and peaks in the occurrence of enamel hypoplasia in caprine populations. In general terms, the future research in this area needs to be focused developing more accurate and detailed development chronologies for caprine teeth.

9.4 General conclusions and future directions

This research has clearly demonstrated that enamel hypoplasia can be recorded and analysed in high-crowned species such as caprines and that it is a potentially powerful tool for investigating a wide range of questions regarding animal husbandry and management in archaeological populations. There are a wide range of archaeological applications for the study of enamel hypoplasia. Given the pilot nature of this research, only a few of these possible applications have been investigated in detail in this thesis.

The potential for enamel hypoplasia to be used to investigate fodder provisioning is clear. Enamel defects can be correlated to seasonal periods of malnutrition in caprine populations and differences occur in periods of nutritional stress between caprines eating a seaweed based diet and those on a terrestrial diet. Consequently there is a clear possibility that enamel defects can be used to specifically investigate seaweed foddering and fodder provision in archaeological populations. This is suggested as an area which may be of particular interest to the North Atlantic regions, where seaweed foddering is well documented but little investigated archaeologically. This research has touched on this issue with regard to the suggestion of foddering in the winter months, potentially with seaweed supplementation in relation to the caprine populations from the Neolithic site of Skara Brae on Orkney.

The ability to use enamel hypoplasia in combination with environmental / climatic / archaeological data to provide information on animal husbandry practices is obviously one of the most interesting aspects of this research. The ability to investigate the timing of birth and weaning in archaeological populations can potentially reveal a wide range of information about archaeological management strategies. This would be of particular interest to investigating enforced weaning and the management of young animals in archaeological populations.

The potential to investigate life histories within archaeological populations, as well as identify variation in the management of animal populations has a range of applications for archaeological research. This has been briefly discussed in this research with regard to the introduction of a new husbandry regime to the Mývatn region of Iceland. Obviously, enamel hypoplasia used in conjunction with archaeological, climatic and biomolecular data could be used to investigate in more detail the complex interaction between site economies, husbandry regimes and the shifting environmental conditions seen in this region of Iceland. This could also be developed in regard to the Kenyan Neolithic, where this research has hinted at the possibility of variation in animal husbandry regimes between rock shelter and open plain settlement.

As demonstrated in other species such as pigs, enamel hypoplasia has the potential to identify other important questions, such as domestication. While this is an area which has not been addressed during the course of this research, there is potential for similar analysis in caprines. The comparison between enamel hypoplasia in wild caprine species and domestic caprine species would be the first step towards this type of investigation and be of great interest, as hypothetically the wild species should show less evidence of enamel defects than the domesticated animals.

Whilst this research has focused on caprines for the various issues outlined, there is significant future potential for this methodology to be extended into other high-crowned species such as cattle and horses, to investigate wider patterns of animal husbandry. It is hoped that this research has provided the groundwork for the future study of enamel hypoplasia in high-crowned species, and has demonstrated the potential for it to be used in conjunction with other techniques to investigate a wide range of important archaeological questions and issues, hitherto not easily explored.

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Appendix 1: Modern Kenya Paper

The influence of environmental factors on enamel hypoplasia in domestic sheep and goats in southern Kenya Masailand.

Marie Balasse [1], Bethan Upex [2] and Stanley H. Ambrose [3]
[1] Muséum national d'Histoire naturelle and CNRS. Département Ecologie et Gestion de la Biodiversité, Paris, France.
[2] University of Durham, Department of Archaeology, Durham, UK
[3] Department of Anthropology, University of Illinois, Urbana, IL, USA

Abstract / Zusammenfassung

Enamel hypoplasia was reported on caprine teeth from Neolithic assemblages in southwest Kenya, where its incidence was thought to vary with husbandry practices. A prerequisite to the interpretation of enamel hypoplasia on assemblages from archaeological pastoral sites is the identification of the environmental causes of this defect in extensive herd management systems. The influence of environmental factors on enamel hypoplasia frequency and severity has never been observed in traditional herd management systems. This study investigated the frequency and severity of enamel hypoplasia in modern sheep and goats from Kenya under known environmental conditions, providing a modern analogue for archaeological samples from this region. Kenya, where minor droughts occur every three to four years, offers a robust framework for the study of recurrent environmental stress and associated enamel hypoplasia in Masai pastoralist domestic herds. The studied sample includes 116 molars collected in 2000, 2001 and 2002 in the semi arid Narok South district and the mesic Central Rift Valley. Results showed the percentage of teeth bearing enamel hypoplasia to be very high (79% in Narok South and 72% in the Central Rift Valley). Both frequency and severity of enamel hypoplasia were higher in the Narok South sample than in the Central Rift Valley sample, reflecting more stress during growth and development in this semi-arid zone. In the Central Rift Valley, a difference in the frequency of hypoplasia was observed between sheep and goats, possibly explained by differences in feeding behaviour and resistance to disease between these species. Unexpectedly, the major drought of 2000 had no impact on hypoplasia frequency or severity, suggesting that enamel hypoplasia in these caprines cannot be explained by nutritional or physiological stress linked to specific drought episodes alone. It is suggested that high levels of enamel hypoplasia in today's populations may be due to infectious parasitic diseases.

Bei Zähnen von Schaf und Ziege aus neolithischen Fundkomplexen im Südwesten Kenias wurden Schmelzhypoplasien festgestellt, deren Häufigkeit auf die damals bestehenden Praktiken der Tierhaltung zurückgeführt wurden. In diesem Beitrag werden die Häufigkeit und der Schweregrad von Schmelzhypoplasien bei modernen Schafen und Ziegen aus Kenia unter bekannten ökologischen Bedingungen untersucht, als modernes Analogon für archäologische Materialien aus derselben Region. Kenia, wo etwa alle drei bis vier Jahre kleinere Trockenperioden auftreten, bietet solide Rahmenbedingungen für das Studium von periodisch auftretenden Umweltbelastungen und den damit verbundenen Schmelzhypoplasien in den Haustierherden des Hirtenvolkes der Masai. Die analysierte Stichprobe beträgt 116 Molaren, die 2000, 2001 und 2002 in dem semi-ariden Narok South District und dem gemäßigt feuchten Central Rift Valley gesammelt wurden. Der Prozentsatz von Zähnen mit Schmelzhypoplasien erweist sich als sehr hoch (79% im Narok South District und 72% im Central Rift Valley). Sowohl die Häufigkeit als auch der Schweregrad der Schmelzhypoplasien sind höher im Material von Narok South verglichen mit dem aus dem Central Rift Valley, was auf ein höheres Maß an Stress während des Wachstums und der Entwicklung in der semiariden Zone zurückzuführen ist. Im Central Rift Valley wurde eine unterschiedliche Häufigkeit der Hyploplasien bei Schaf und Ziege festgestellt, welche vielleicht auf Differenzen im Nahrungsverhalten oder einer unterschiedlichen Resistenz gegenüber Krankheiten beruht. Als unerwartet stellte sich heraus, dass sich die große Dürre im Jahr 2000 weder auf die Häufigkeit noch auf den Schweregrad von Hypoplasien ausgewirkt hat. Demnach treten Schmelzhypoplasien bei Schaf und Ziege nicht einzig und alleine als Folge von Ernährungs- oder physiologischerm Stress, verbunden mit bestimmten Dürreperioden, auf. Als mögliche Ursache für die hohe Inzidenz von Schmelzhypoplasien in den heutigen Populationen kommen infektiöse parasitäre Erkrankungen in Frage.

Keywords: Enamel hypoplasia, sheep, goat, pastoralism, drought, Kenya, Masailand
Schmelzhypoplasien, Schaf, Ziege, Pastoralismus, Dürre, Kenia, Masailand

Introduction

Enamel hypoplasia is a quantitative defect, produced by an interruption or disturbance in the formation of the organic matrix of enamel (Suckling 1980). The occurrence of enamel hypoplasia has been associated with developmental stress (birth, weaning), nutritional stress, infectious disease, parasite infestation, fluoride toxicosis and traumatic injuries (Suckling et al. 1983, 1986; Kierdorf et al. 1993; Dobney et al. 2004; Franz-Odendaal 2004; Skinner & Hopwood 2004). Hypoplasia is visible on the tooth crown as a thinning of the enamel layer forming lines or pits in the surface enamel. Its position on the crown relates to the tooth development stage at the time when the stress occurred (Suckling & Cutress 1977) and its severity is linked to the intensity of the stress episode (Suckling et al. 1986).

Enamel hypoplasia is a useful marker of stress in ancient populations. It has been widely used by anthropologists to infer the health status of modern and past human populations (Skinner & Goodman 1992) and was more recently applied to archaeological domestic animal populations (Gifford-Gonzalez & Kimengich 1984; Gifford-Gonzalez 1985; Marshall 1990a; Ervynck & Dobney 1999; Dobney & Ervynck 2000; Dobney et al. 2002, 2004; Clavel & Sicard 2007).

In East-Africa, enamel hypoplasia was reported on caprine teeth from Neolithic (1st millennium BC) assemblages from southwest Kenya, where its occurrence was tentatively linked to differences in husbandry practices. Early analyses by Gifford-Gonzalez suggested that the occurrence of hypoplasia in caprines was high in the Elmenteitan assemblage of Masai Gorge Rockshelter compared to what was observed in the Savanna Pastoral Neolithic assemblages of Narosura and Prolonged Drift. The author suggested this could be due to differences in herding practices between both cultural entities (Gifford-Gonzalez & Kimengich 1984; Gifford-Gonzalez, 1985). Similarly, Marshall (1990a) reported a fairly high incidence of hypoplasia in the caprine assemblages of Ngamuriak (Elmenteita) and a moderate frequency in the smaller assemblage of Lemek North-East (Savanna Pastoral Neolithic). Preliminary observations on the sheep and goat teeth from Enkapune Ya Muto and Enkapune Ya Sauli seem to confirm a high incidence of hypoplasia in these Elmenteitan assemblages, although on a very limited number of teeth analyzed (Balasse, unpublished data). A re-examination of the Neolithic archaeological collections from Southwestern Kenya, with systematic study of hypoplasia frequency, severity and distribution would help in defining the health states and potential seasonal stresses of Neolithic caprine herds, for a better characterization of the subsistence strategies of those Neolithic communities heavily dependent on pastoral resources (Ambrose 1984; Robertshaw 1988, Marshall 1990b; Gifford-Gonzalez 1998).

However, a prerequisite to the interpretation of hypoplasia on assemblages from archaeological pastoral sites is the identification of the potential environmental causes of this defect in extensive herding systems. Although sheep have served as a model in several experiments investigating the aetiology of enamel hypoplasia (Suckling 1980, Suckling & Cutress 1977; Suckling et al. 1983, 1986), the influence of environmental factors on sheep enamel hypoplasia has never been studied in traditional herd management systems. Kenya offers a robust framework to study recurrent environmental stress and associated enamel hypoplasia in domestic caprine herds. Major droughts occur every decade and minor droughts every three to four years (UNEP/GoK 2000; Orindi et al. 2007; Lasage et al. 2008; Speranza et al. 2008), with consequences for the nutritional and health states of domestic livestock. Used to the unpredictable nature of arid lands, pastoral groups have developed coping strategies in response to these drought events (Ryan et al. 2000; Orindi et al. 2007; Mworia & Kinyamario 2008). In spite of these coping strategies, droughts severely affect large numbers of livestock, among which cattle suffer the most (UNEP/GoK 2000). Sheep and goats are affected to a lesser extent by water deprivation and the loss of grassy resources. Their survival implies that they pass through the stress episodes and subsequently may record them in their growing teeth.

The aims of this study were to a) investigate if the semi-arid zone of Narok South District and the more mesic habitats of the Central Rift Valley highlands and lowlands in Kenya produce differences in the frequency and severity of enamel hypoplasia; b) evaluate the impact of the major drought of the year 2000 on the health status of animals in these regions as reflected in enamel hypoplasia frequency and severity, and c) investigate if sheep and goat respond differently to environmental pressures in terms of enamel hypoplasia.

Material

The caprine tooth rows were collected from freshly slaughtered animals and the refuse dumps of Masai villages in two main regions of southwest Kenya: the Narok South District between the eastern edge of the Loita Plains and the western edge of the southern Rift Valley, and the Narok North and Nakuru districts on the west side of the Central Rift Valley (Fig. 1). The study area falls within the Intertropical Convergence Zone, characterized by two wet seasons. The long rains occur from late March to early June and the short rains during late October to early December. Rainfall in the

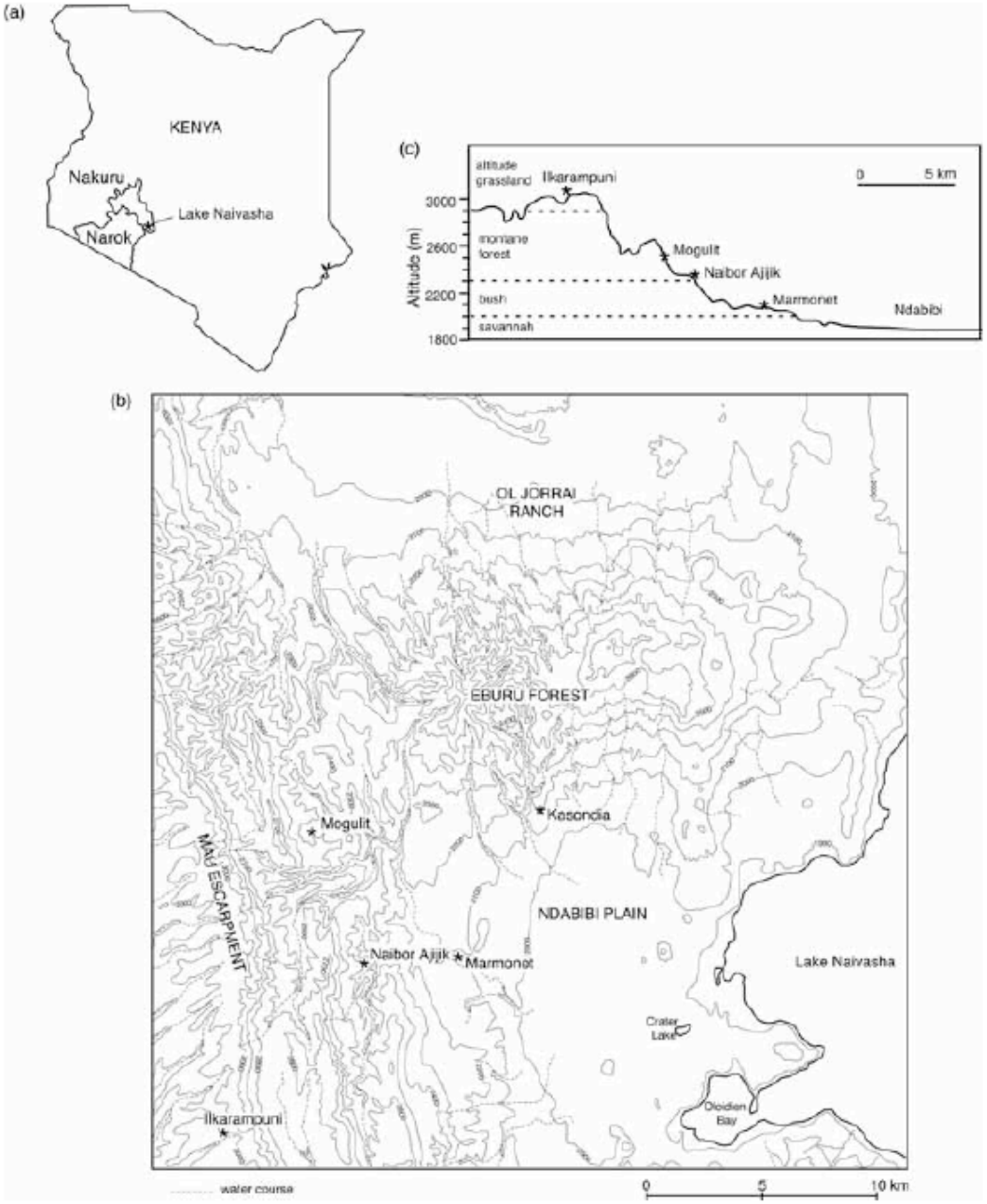

Fig. 1: The study area. (a) Location of Narok and Nakuru Districts and Lake Naivasha in the Central Rift Valley in Kenya. (b) Topography of the study area in the Central Rift and location of the villages (after Map DOS 2797, Kenya Government 1977). (c) Schematic profile of the eastern slope of the Mau escarpment showing the elevation-stratified ecozones (modified from Ambrose & Sikes 1991) and location of the villages.

Nakuru basin of the Central Rift Valley study area is weakly trimodal, with slightly elevated rainfall during July and August (Davies et al., 1985).

The study was conducted on 56 domestic caprines comprising 23 sheep, 23 goats and 10 individuals whose specific status could not be securely determined. The goats belong to the Small East African breed and Red Masai sheep were predominant in both districts. Merino and Black Headed Somali sheep breeds were also present in the herds from Narok South District. A total of 116 molars were included in the analysis, collected over June and July 2000, 2001 and 2002. In the year 2000, Kenya experienced a severe drought, resulting from the failure of four consecutive rainy seasons over a period of two years (UNEP/GoK 2000). The semi-arid and arid lands were most affected by the drought, and Narok South District suffered more severely than the Central Rift. The majority of the tooth rows collected are from individuals aged between 2 and 4 years. As caprine permanent molars are formed during the first two years of life (Weinreb & Sharav 1964), many of the individuals sampled had teeth that were developing in the year 2000, allowing investigation of the intensity of the stress induced by the drought.

Central Rift Valley

The villages included in the Central Rift Valley are located in the Narok North and Nakuru administrative districts on the west and north sides of the Naivasha basin and on the slopes of the Mau Escarpment and Mt. Eburu (Fig. 1). The mean annual rainfall decreases from 1600 mm on top of the Mau at 3100 m to less than 600 mm on the valley floor at 1900 m. At high elevations, low temperatures (annual mean 11°C) increase rainfall effectiveness, contrasting with the semi-arid conditions of the valley floor. This climatic gradient influences the vegetation cover and Masai herding practices (Balasse & Ambrose 2005a). Large areas of the Central Rift are fenced for large-scale wheat and barley agriculture, small farms and farming settlement schemes, private game reserves and the Mt. Eburu Forest Preserve. These areas are mainly located at lower elevations, limit access to pastures for domestic stock, and promote overgrazing of accessible areas. Access to natural sources of salt is also limited. Supplementary soda lake evaporite mineral salt (Magadi soda) is purchased when funds and transportation are available.

Domestic sheep and goats from the Ndabibi Plains (1936 m) and Marmonet village at the foot of the escarpment (2075 m) are herded all year round in the open to lightly wooded savanna acacia grassland of the Naivasha basin. Piping of water from the highlands down to the valley floor and the use of wells allow the herds to spend the dry season on the semi-arid grasslands. Kasondia (2224 m) is situated on the lower slope of Mt. Eburu, and Naibor Ajijik (2400 m) is on the Mau Escarpment close to the lower limit of the montane forest. Both villages are located in a mixed olive-leleshwa-acacia (*Olea africana*, *Tarchonanthus camphoratus*, *Acacia* spp.) bushy environment of the ecotone between savanna and montane forest. In both locations, goats browse in the vicinity of the villages. Sheep graze on the valley floor (Ndabibi Plains) although in drier conditions they are moved to higher elevations.

Mogulit is located at mid elevation (2492 m) on the Mau Escarpment in the montane forest (*Juniperus* and *Podocarpus*) zone. The pasture area for caprines changes annually in a circuit within the montane forest zone that brings them back to the vicinity of the village every few years. Some herds are taken to a lower elevation in the bush.

The top of the Mau Escarpment is covered with open grassy moorlands. At Ilkarampuni (2994 m) sheep and goats stay in the highlands all year round, despite low temperatures during the rainy seasons.

Loita Plains

Enkorika, Oloisukut and Olengoluo are located in the semi-arid ecological zone (600 mm average annual rainfall) between the eastern margin of the Loita Plains (~2000 m) and the western margin of the southern Rift Valley (1600 m) within the Narok South District in grassland savanna and shrub vegetation (Fig. 2). In contrast to the Central Rift, land is held communally. Pastures are not fenced, and farm gardens comprise an insignificant proportion of the landscape. Salt is readily available in salt springs at the headwaters and along the Olonganaiyo River, which forms the southern boundary of the Olengoluo and Oloisukut locations.

Enkorika (1683 m) is located near the western margin of the southern Rift Valley on the Oletugathi Ridge, which forms the divide between the Ewaso Ngiro and Siyabei river valleys (~1540 m). In the main dry season, sheep are transferred to Ol Jorrai (2100 m), at the base of the northern slopes of Mt Eburu on the southwest side of the Lake Nakuru basin in the Central Rift Valley (Nakuru District) in February and brought back to Enkorika in December. Herds at Ol Jorrai have access to natural salt sources at Lake Elmenteita and in exposures of salt-bearing lacustrine sediments. Goats spend the rainy seasons in the vicinity of Enkorika and during the dry seasons are herded higher into the hills. Sheep and goats from Oloisukut (1700 m) are herded together in the surrounding Loita Plains throughout the year. At Olengoluo (1818 m) the few sheep spend the whole year in the vicinity of the village while goats are herded with cattle in the surrounding Loita Plains, except during

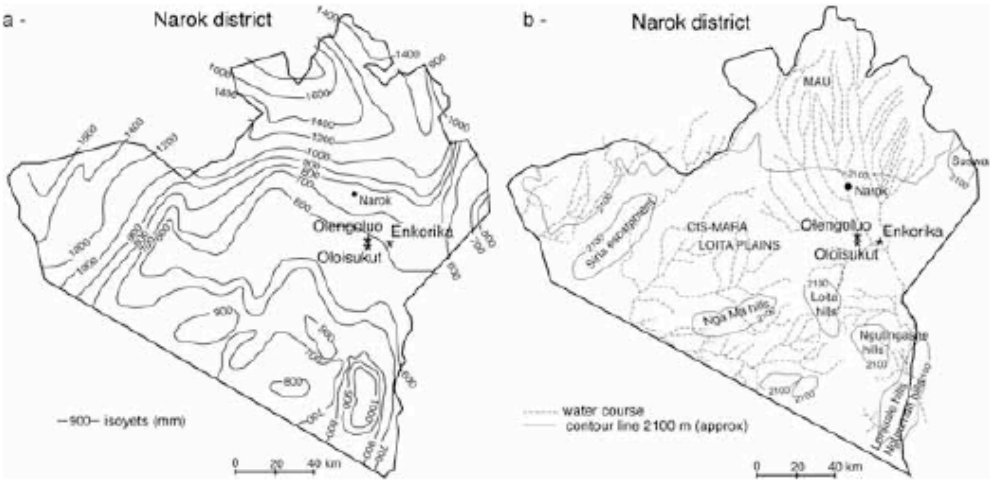

Fig. 2: The Narok South study area. (a) Average annual rainfall in Narok District (after Ogutu, 1999). (b) Topography and drainage of Narok District, with location of the villages (after Ogutu 1999).

the wildebeest birthing season (April to June) when they are brought higher up on the hills and down to the Ewaso Ngiro, Olonganaiyo and Ntuka river valleys to prevent domestic cattle from contracting bovine malignant catarrhal fever (Gifford-Gonzalez 2000).

This description of land use and herd management practices by the Masai in the Central Rift Valley and Narok South District was obtained from discussions with local herders and field observations taken over the period of teeth collection. Practices may differ from one year to another according to climatic parameters and their consequences for the availability of water and pastures, and may also differ between herders depending on interfamily alliances.

Methods

When the slaughter of the animal was witnessed, the teeth were securely identified as belonging to either sheep or goat. In all other cases, the species was identified using morphological criteria on the lower premolars and molars (after Payne 1985; Helmer 2000; Halstead et al. 2002; Balasse & Ambrose 2005b). The upper tooth rows and one lower first molar (Nai o/c8) could not be identified as sheep or goat; they appear in the analysis as unidentified caprines. By using species separation, tooth development and wear stages, all mandibles were demonstrated to belong to different individuals.

Enamel hypoplasia was observed on all three molar crowns and was recorded on all cusps, on the buccal side of the lower teeth and the lingual side of the upper teeth. The measurements include (Fig. 3):

1 - Height of the anterior lobe (H), transversal diameter (dt), and wear stage (Payne 1973)

2 - Occurrence of any defect (line, depression or pit) and its position in the tooth (distance from the crown-root junction) on both lobes

3 - Severity of the lines, coded from 1 to 4. A line coded 1 can be observed only under strong directional light. Code 2 can be clearly observed without strong lighting. Code 3 corresponds to a more severe defect, and code 4 is close to aplasia (Fig. 3). Depressions are coded 1.

Age at death was estimated from the molars developmental stage (Weinreb & Sharav 1964), tooth wear index (H /dt ratio: Helmer 1995; Blaise 2006) and tooth wear pattern (Payne 1973). When age estimations from tooth wear and tooth development disagreed, tooth developmental stage was considered more accurate. The chronology of tooth formation in goat was assumed to be the same as in sheep, given that the ages of tooth eruption are similar in both species (Silver 1970). The chronology of tooth formation was assumed to be the same for lower and upper molars. The very first stages of development of the lower first and second molars were observed to start slightly earlier than in corresponding upper molars but the difference was very small (Witter & Mizek 1999). Although no significant difference in the development of lower and upper teeth was mentioned by Milhaud & Nezit (1991) in their study of the Préalpes du Sud sheep breed, a slightly more developed state of growth of lower compared to upper molars was sometimes observed in other sheep breeds (MB, pers. observation). Although this delay is

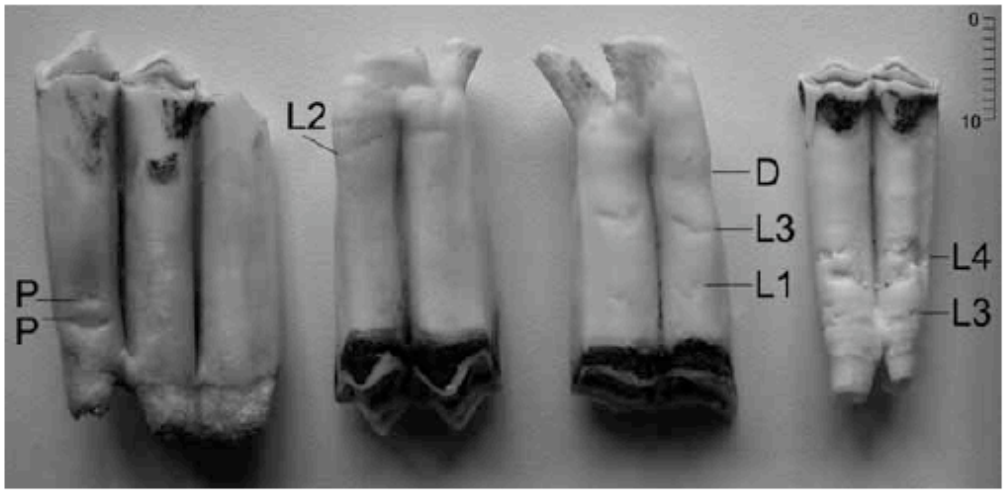

Fig. 3: Typology of enamel defect and severity code. Pit (P), depression (D) and line (L severity). L1: Line coded 1. Scale in mm.

not well documented because of its variability, we estimate it is no larger than inter-individual variability in the timing of growth in lower molars, especially the third molar. Nevertheless, this variability is taken into account when comparing localisation of enamel hypoplasia in the lower and upper teeth.

The period (date) of formation of the teeth was calculated from the estimated age at death, the chronology of tooth growth (Weinreb & Sharav 1964) and the date of collection assuming that all animals died shortly before the date of collection, as suggested by the preservation of bone.

Results

A total of 178 hypoplastic enamel defects were observed, of which 71% are lines, 22% are depressions (as defined by Dobney & Ervynck 1998), and 6% are pits (Table 1). In 37 cases (21%), the hypoplasia could be observed only on one lobe of the tooth. In a majority (70%) of these 37 cases, the hypoplasia could be observed only on the anterior lobe. Of these isolated hypoplasia events, 43% are lines, 38% are depressions and 19% are pits. Some of them, particularly the pits, could be interpreted as resulting from local trauma (Suckling & Cutress 1977; Suckling 1980). However, recent studies have suggested that localized hypoplasia (pits) could also be due to systemic stress (Franz-Odendaal 2004) and for this reason they are included in the analysis. The reason for the occurrence of these isolated defects is not understood. They cannot always be attributed to a delay in the deposition of the enamel matrix in both lobes, as they are not necessarily located in the lower or higher part of the crown but occur in any part of it: they were located at 1 mm to 25 mm from the crown root junction on the anterior lobe, at 1 to 18 mm from the crown root junction on the posterior lobe. Reduced observational visibility of the enamel on one lobe, due to cementum deposits may be responsible for some of these single defects.

A histological study might be required to confirm whether they are really absent from one lobe. As many individuals do not have all three molars present the frequency of hypoplasia is expressed as the number of hypoplastic defects per tooth rather than per individual. This raises the possibility of multiple representations of the same stress event in a single individual across the molar crowns. For example, the second half of the first molar (M1) forms at the same time as the first half of the second molar (M2) crown (Weinreb & Sharav 1964; Table 2). Hypoplastic defects present at both locations should therefore reflect the same stress event. This effectively doubles the chance of this single physiological event being represented when the M1 and M2 from the same tooth row are present in the assemblage. Among the 31 individuals included in the analysis with both M1 and M2 present, 16 have hypoplasia on both teeth. The position of these hypoplastic defects is shown in Table 3. Of these, only six hypoplasias were present in the first half of the M2 crown, demonstrating that the number of stress events potentially represented twice in the dataset is very low.

The percentage of tooth crowns showing hypoplastic enamel defects is 79% in Narok South district and 72% in the Central Rift Valley. Of the 28 individuals represented by two molars (M1 and M2 or M2 and M3), 26 (93%) show defects in at least one tooth, and 13 (46%) in both teeth. Of the 16 individuals represented by the

Central Rift		M1			M2			M3		
individual	species	L	D	P	L	D	P	L	D	P
Kat capra 1	goat				0	0	0	0	0	1
Mar capra 1	goat	1	0	0	0	0	0			
Nai capra 1	goat				1	1	0	0	1	0
Nai capra 2	goat	0	1	0	0	0	0	1	0	0
Nai capra 3	goat	1	1	0	0	0	0			
Ilk o/c 2	goat?	0	0	0	0	0	0	0	0	0
Ilk o/c 6	goat?	0	1	0	0	1	0			
Kat o/c 1	goat?	0	1	1	1	0	0	0	0	2
Nai o/c 1	goat?				0	0	0	0	0	0
Nai o/c 2	goat?	0	0	0	0	0	0			
Nai o/c 3	goat?							2	1	0
Nai o/c 4	goat?							0	0	0
Nai o/c 7	goat?				0	0	1	1	1	0
Nda o/c 1	goat?	0	1	0	1	0	0	1	0	0
Nda o/c 2	goat?	0	0	0						
Mar ovis 1	sheep	1	0	0						
Nai ovis 1	sheep				1	0	0	4	0	0
Nai ovis 2	sheep				3	0	0	2	0	0
Nai ovis 3	sheep				0	0	0			
Nda ovis 1	sheep	0	0	0						
Ilk o/c 1	sheep?	0	1	0	0	0	0			
Ilk o/c 3	sheep?				2	0	0	2	0	0
Ilk o/c 4	sheep?				1	0	0	0	0	0
Ilk o/c 5	sheep?				0	2	0	0	1	0
Ilk o/c 7	sheep?	0	0	0	1	0	0	4	0	0
Ilk o/c 8	sheep?				1	0	0	0	0	0
Kat o/c 2	sheep?	2	0	0						
Mar o/c 1	sheep?	1	0	0	2	0	0	3	0	0
Mog o/c 1	sheep?	2	1	0	0	3	1	0	0	0
Mog o/c 2	sheep?	2	0	0	0	0	0	1	0	0
Mog o/c 3	sheep?	0	0	0	1	0	0	1	0	0
Nai o/c 5	sheep?				3	0	0	2	0	1
Nai o/c 6	sheep?				2	1	0	2	0	0
Nai o/c 8	unid	2	0	0						
Ilk o/c9*	unid	0	1	0	1	0	0			
Ilk o/c10*	unid	2	0	0	0	1	0			
Mog o/c4*	unid	1	0	0	2	1	0	1	1	0
Mog o/c5*	unid	1	1	0	4	0	0	2	0	0
Nai o/c9*	unid				1	0	0			
Kat o/c3*	unid	0	1	0	0	0	0			

Table 1: a- Central Rift Valley. Occurrence of lines (L), depressions (D) and pits (P) in the first (M1), second (M2) and third molars (M3) of sheep, goats, and unidentified domestic caprines (unid). *: species identified from morphological criteria; **: upper teeth. Villages: Kat: Kasondia; Mar: Marmonet; Nai: Naibor Ajijik; Ilk: Ilkarampuni; Nda: Ndabi-bi plain; Mog: Mogulit; Enk: Enkorika, Ole: Olengoluo; Oloi: Oloisukut.

Narok South		M1			M2			M3		
individual	species	L	D	P	L	D	P	L	D	P
Enk capra 1	goat	0	2	0	3	0	0			
Enk capra 2	goat	0	0	0	3	0	0			
Enk capra 3	goat	1	0	0	0	2	1			
Enk capra 4	goat	3	1	0	4	0	0	5	0	0
Ole capra 1	goat	0	0	0	0	0	0			
enk o/c 1	goat?	3	0	0	1	1	1	4	1	0
Ole o/c 2	goat?				1	0	0	1	1	0
Oloi o/c 1	goat?	0	0	0	1	0	1			
Ole ovis 1	sheep				0	2	0			
enk o/c 2	sheep?	2	0	0						
enk o/c 3	sheep?							3	0	0
Ole o/c 1	sheep?	3	0	0	0	1	0	0	0	0
Oloi o/c 2	sheep?	3	0	0	4	0	0	3	0	0
Enk o/c4*	unid	0	0	0	2	0	0			
Enk o/c5*	unid	0	2	0	3	0	1	1	0	0
Oloi o/c3*	unid	0	2	0	0	0	0			

Table 1: b- Narok South. Occurrence of lines (L), depressions (D) and pits (P) in the first (M1), second (M2) and third molars (M3) of sheep, goats, and unidentified domestic caprines (unid). *: species identified from morphological criteria; **: upper teeth. Villages: Kat: Kasondia; Mar: Marmonet; Nai: Naibor Ajijik; Ilk: Ilkarampuni; Nda: Ndabibi plain; Mog: Mogulit; Enk: Enkorika, Ole: Olengoluo; Oloi: Oloisukut.

Age	M1	M2	M3	Main lifetime events
birth	One half of crown formed	Absent	Absent	Birth
3-6 months	Two thirds of crown formed	One third of crown formed	Absent	Weaning (3-4 months)
9 months	Crown formation complete	Crown still forming	Absent	
12 months		Crown formation complete	Bud visible	First gestation (9-12 ms) First lactation (14-17 ms)
18-24 months			Crown almost complete	

Table 2: Development stages of the first (M1), second (M2) and third lower molars (M3) of sheep (data from Weinreb & Sharav 1964) and corresponding main lifetime events.

three molars, only one showed no hypoplasia, 15 (94%) show hypoplastic defects on at least two molars, and 9 (56%) show hypoplastic defects in all three molars (Table 1).

The frequency and severity of enamel hypoplasia are shown in Table 4, according to species, location (Narok South/Central Rift), and the type of environment (high-altitude grassland / montane forest / savanna-bush). Because part of the herds from Naibor Ajijik and Kasondia spend some time on the Rift Valley floor, they are grouped with the herds from Marmonet and Ndabibi in the "savanna-bush" group. The frequency of enamel hypoplasia for all caprines considered together is higher in Narok South than in the Central Rift (Fig. 4a) and this difference is statistically significant (Chi-Squared test, χ^2=13.27, p = 0.001; results from statistical tests are shown in Appendix 1). In the Central Rift the frequency of enamel hypoplasia is higher in sheep than in goat (Fig. 4b), even though this difference is not

individual	species	position of defect in M1	position of defect in M2
Enk capra 1	goat	9.42 ; 4.74*	17.24 ; 12.51 ; 8.67
Enk capra 3	goat	6.49	18.28* ; 10.96 (pit) ; 5.49
Enk capra 4	goat	10.64 ; 10.05 ; 4.46 ; 2.87	**19.71** 15.99 11.34 5.03
Enk o/c 1	goat?	7.67 ; 5.38 ; 2.85	16.07 (pit) ; 12.71 ; 2.26
Enk o/c 5	unid.	12.56 ; 3.92	17.96 ; 13.63 ; 8.92 (pit) ; 8.57
Ilk o/c 6	goat?	7.89	18.54
Ilk o/c 9	unid.	6.45	5.77
Ilk o/c 10	unid.	7.45 ; 3.21	9.09
Kat o/c 1	goat?	5.63* ; 1.12* (pit)	15.55
Mar o/c 1	sheep?	3.3	2.62 ; 1.58*
Mog o/c 1	sheep?	12.27 ; 6.45 ; 3.93	**28.96*** ; **23.1*** ; 13.69* (pit) ; 9.59*
Mog o/c 4	unid.	5.77 ; 3.6	**21.21** ; 15.73 ; 9.62
Mog o/c 5	unid.	5.23 ; 1.83*	15.49 ; 7.52 ; 4.44 ; 1.03
Nda o/c 1	goat?	9.2	4.54
Ole o/c 1	sheep?	13.94 ; 8.84 ; 5.63	10.92
Oloi o/c 2	sheep?	13.94* ; 11.47 ; 9.3 ; 1.87	**26.19** ; **21.18** ; 15.53 ; 8.61 ; 3.52

Table 3: Position of defect in the first (M1) and second molars (M2) of individuals bearing both teeth. * Position recorded on lobe 2. In Bold: stress event recorded in M2 and suspected to be represented also on M1.

Frequency	Central Rift			Narok South			Central Rift		
class	goat	sheep	all	goat	sheep	all	alt grassland	montane forest	savannah-bush
0	13	9	23	4	1	7	7	3	13
1	12	11	29	2	1	4	10	4	15
2	5	8	18	3	2	8	4	4	10
3	1	6	8	5	4	9	0	2	6
4	0	3	4	2	1	4	1	2	1
5	0	0	0	2	0	2	0	0	0
N	31	37	82	18	9	34	22	15	45
Severity	**Central Rift**			**Narok South**			**Central Rift**		
class	goat	sheep	all	goat	sheep	all	alt grassland	montane forest	savannah-bush
1	13	23	47	12	5	23	14	12	20
2	5	20	33	15	5	21	4	10	21
3	1	7	12	4	7	13	2	3	6
4	1	5	6	7	4	12	2	0	4
N	20	55	98	38	21	69	22	25	51

Table 4: Frequency and severity of hypoplasia in sheep and goats from the Central Rift Valley and Narok South district, and in domestic caprines from different ecozones in the Central Rift (high altitude grassland; montane forest, savanna-bush).

highly significant (χ^2=13.27, p = 0.06). The difference between both species is not significant in Narok South District. The severity of hypoplasia for all caprines is higher in Narok South than in the Central Rift (Fig. 4c) and this difference is significant (χ^2=8.14, p = 0.04), but within each region it is not significantly different between sheep and goat. The frequency and severity of enamel hypoplasia between the elevation zones (high-altitude grassland / montane forest / savanna-bush) in the Central Rift are not significantly different.

The distribution of enamel hypoplasia on the crown of each molar was investigated using the anterior lobe, because the frequency of hypoplasia was higher than on the posterior lobe. The distributions are shown in Fig. 5. The graphs showing M1, M2 and M3 for sheep and goats are created using only lower teeth, and the graphs compiling the data for all caprines include both lower and upper teeth combined. The distribution of enamel hypoplasia is similar in sheep and goat. On the first molar in goats, hypoplastic defects are exclusively

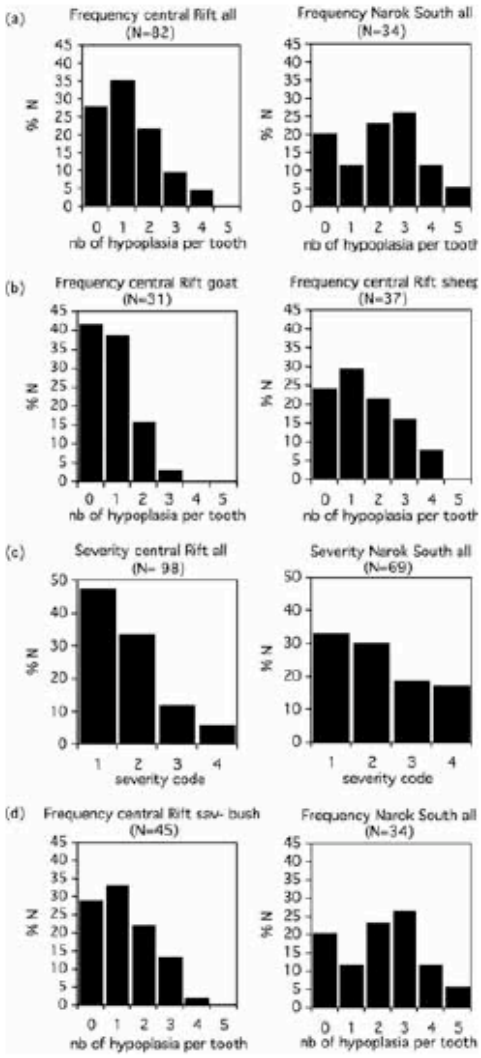

Fig. 4: Frequency and severity of hypoplasia in subsamples from Narok South District and the Central Rift Valley.

located in the most cervical 12 mm of the crown, and only two defects were recorded higher in the crown in sheep (Fig. 5a). In the second molar, hypoplasia appears almost exclusively over the cervical half of the crown in both species, although some rare defects are observed in the middle of the crown (Fig. 5b). On the third molar, hypoplasia is evenly distributed over the most cervical two thirds of the crown (Fig. 5c).

Estimation of the growth period for each tooth crown is shown in Appendix 2. The developmental period covered by the specimens is 1994 to 2002, although the number of teeth developed before 1995 and after 2001 is very low and for this reason they are not included in the analysis. Results for the frequency and severity of hypoplasia in years 1995 to 2001 are shown in Table 5.

Discussion

Frequency of enamel hypoplasia

The overall frequency of enamel hypoplasia observed in the domestic caprine herds from Narok South and the Central Rift seems high, although we lack analogous modern material for adequate comparison. Most studies of the occurrence of enamel hypoplasia in animal populations have been conducted on wild species (Skinner 1986; Guatelli-Steinberg & Skinner 2000; Kierdorf et al. 1993; Franz-Odendaal 2004; Niven et al. 2004). Published analyses of enamel hypoplasia in domestic stock involve archaeological populations of pigs from North Western Europe (Ervynck & Dobney 1999; Dobney et al. 2004; Clavel & Sicard 2007), and caprines from archaeological sites in southwest Kenya (Gifford-Gonzalez & Kimengich 1984; Gifford-Gonzalez 1985; Marshall 1990). Although the occurrence of enamel hypoplasia reported in the studies of archaeological caprine teeth from Kenya was quantified in a different manner (percentage of tooth rows, or percentage of minimum number of individuals bearing enamel hypoplasia), it does not appear to be as high as those reported in this study. It is possible, however, that these previous observations only included the most severe defects.

The frequency of enamel hypoplasia in the caprine herds used in this study is higher than would be expected for drought episodes with a frequency of three to four years, which occur in Kenya (UNEP/GoK 2000; Orindi et al. 2007; Lasage et al. 2008; Speranza et al. 2008). Other causes might be involved, including infectious diseases, reported to be a major cause of mortality in sheep and goat in Kenya (Peeler & Wanyangu 1998) and which might therefore be responsible for at least part of the severe stresses leading to enamel hypoplasia production.

Distribution of enamel hypoplasia on the molars crowns

Table 2 shows the chronology of development of the first (M1), second (M2) and third (M3) lower molars in sheep and the principle life history events occurring during the period of tooth development. According to this chronology, if any of these events caused severe physiological stress, birth would be recorded by hypoplasia in the occlusal third of the M1 crown, weaning (at 3-4 months) in the central third of M1 crown and in the occlusal third of M2 crown, the first gestation (9-12 months: Kosgey et al. 2008) in the cervical third of the

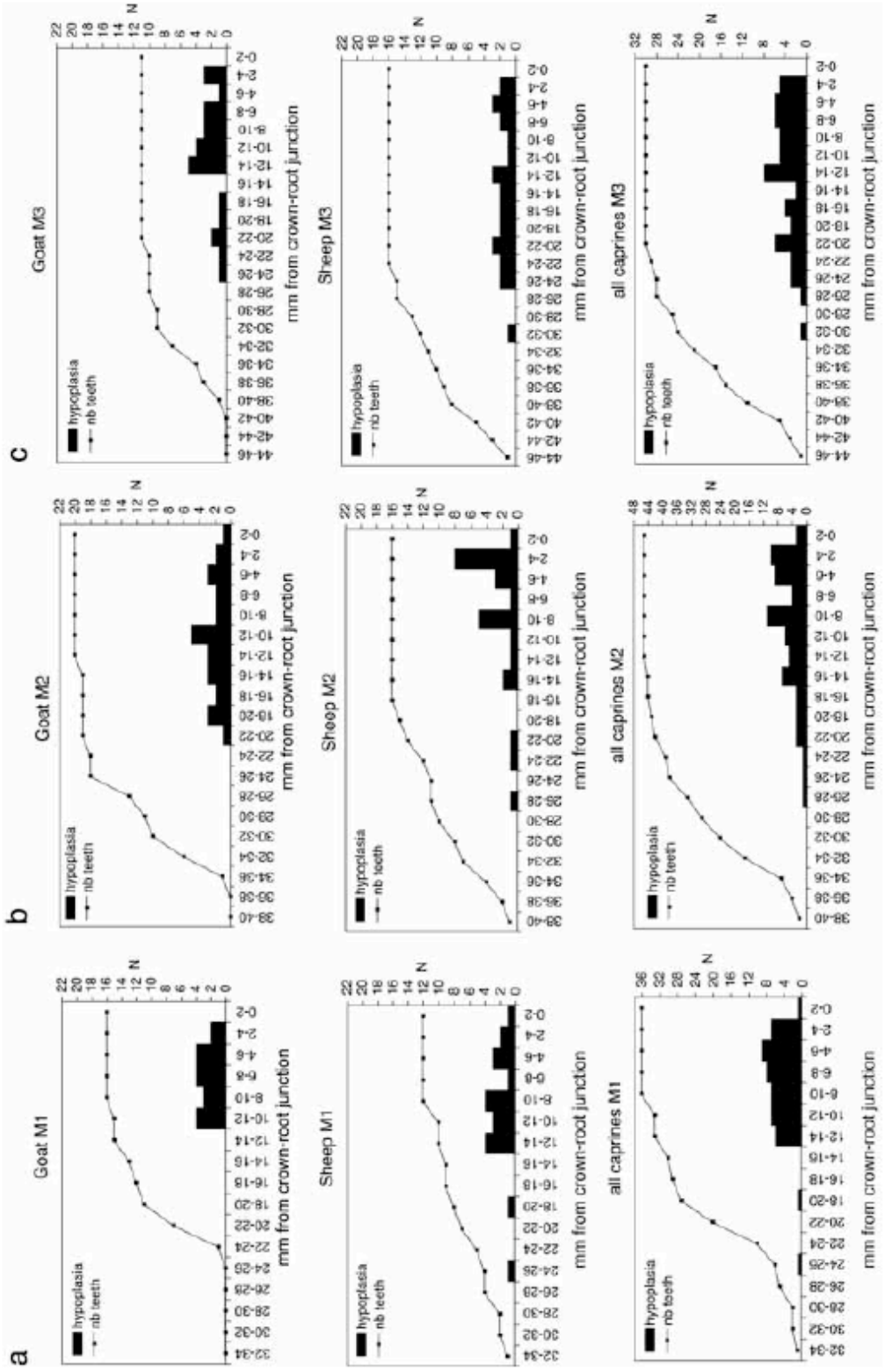

Fig. 5: Localisation of hypoplasia in the lower first (M1), second (M2) and third molars (M3) of sheep, goats, and all domestic caprines (including upper and lower teeth).

Frequency	Central Rift							Narok South					
class	1995	1996	1997	1998	1999	2000	2001	1996	1997	1998	1999	2000	2001
0	5	11	11	10	36	16	9	4	4	8	7	8	3
1	2	0	2	7	10	11	2	0	1	1	1	4	3
2	0	4	1	3	5	5	1	0	1	2	4	2	3
3	1	1	1	3	1	0	0	0	1	2	1	1	1
4	0	0	0	1	2	0	0	0	0	0	2	1	1
5	0	0	0	0	0	0	0	0	0	0	0	1	0
N	8	16	15	24	54	32	12	4	7	13	15	17	11
Severity	Central Rift							Narok South					
class	1995	1996	1997	1998	1999	2000	2001	1996	1997	1998	1999	2000	2001
1	0	2	4	11	19	6	4	0	1	4	8	4	6
2	1	6	1	11	8	8	0	0	1	6	5	6	3
3	3	0	0	2	3	3	0	0	3	1	4	4	1
4	0	1	2	1	1	1	0	0	0	0	1	6	5
N	4	9	7	25	31	18	4	0	5	11	18	20	15

Table 5: Frequency and severity of stress from 1995 to 2001 in the Central Rift and Narok South district.

M2 crown and in the M3 crown, and the first lactation in the M3 crown. The actual distribution of observed enamel hypoplasias does not follow this prediction. Some of the enamel hypoplasias observed in the cervical third of the M2 crown and in the M3 crown might reflect gestation and lactation, although it is not possible to distinguish females from males in caprine teeth. This suggests that most of the stresses recorded in these individuals were caused by environmental factors rather than developmental physiology.

Hypoplastic defects are evenly distributed over the cervical halves of the crowns. If some of the stress episodes were to be linked to seasonal deterioration of environmental conditions, a distribution of hypoplastic defects mimicking that of the seasonal cycle could be expected. However, the chronology of seasonal event may be masked by the pattern of birth seasonality. From the information collected in the field, although a peak of goat births occurs in June-July, kids are born throughout the year. When sheep birthing is scheduled, it occurs during the rainy seasons, in October to December and in March-June. Consequently the animals can reach the dry seasons with different stages of tooth crown development and subsequently might record enamel hypoplasia linked to the same seasonal stress events on different parts of the molar crown.

In the arid and semi-arid zones of Kenya, the reported pre-weaning mortality rate is 10 to 30% in lambs and 20 to 30% in kids (Peeler & Wanyangu 1998). This suggests that the first four months of life of domestic caprines are extremely stressful in these husbandry regimes. However, enamel hypoplasias are rare in the parts of the crown representing these chronologic periods. This lack of obvious representation of early life stress is not easily explained by the fact that this part of the crown is less well represented in the assemblage due to attrition, as it is still represented (Fig. 5). The development and internal architecture of the dental tissues might be the reason for this real absence of enamel hypoplasia in the upper parts of the crown. Histological analysis on this study material is currently in progress, to further investigate this observation.

Differences between the Central Rift and Narok South District

The fragile equilibrium of the herding system in the semi-arid climate of Narok South District is reflected in a higher frequency and severity of enamel hypoplasia in the caprine herds from Narok South than those from the Central Rift. Moreover, the caprines herded in the open savanna to bushy grasslands in the Naivasha basin suffer less stress (environmental, nutritional, physiological) than those from the shrublands of Narok South (Fig. 4d; difference statistically significant, $\chi^2 = 9.19$, $p = 0.01$) although they have similar mean annual rainfall (600 mm). This might be explained in part by the fact that the range of elevation of the Central Rift is higher (1900-3100 m) than in Narok South (1540-2100 m). During dry episodes, altitudinal mobility in search for wetter and cooler conditions is facilitated in the Central Rift by the close proximity to the reliable water supplies and riparian and montane forests and woodlands of the Mau Escarpment, Mt. Eburu and Lake Naivasha. The Masai communities of the Central Rift were all part of intra- or interfamily alliances ensuring a diversity of solutions to face the fluctuations in environmental conditions. Flexibility of the herding system

might similarly explain the absence of significant differences in the frequency and severity of enamel hypoplasia observed in the different ecozones along the elevation gradient in the Central Rift. Such alliances also exist in the herder communities in Narok South District, but the transfer of animals is done over longer distances before more favourable environmental conditions are encountered, as for example, between Enkorika and Ol Jorrai (83 km). The stress of such long distance movements could also be the cause of some of the enamel hypoplasia.

If infectious diseases were responsible for a significant number of the enamel hypoplasia, differences between both districts could be explained by a higher proportion of exogenous sheep breeds (Merino and Black headed Somali) in Narok South District, which are less resistant to diseases and less tolerant to heat and drought than indigenous Red Masai sheep and Small East African goat (Schoeman 2000; Kosgey et al. 2008). However the fact that the Small East African goat, present in both districts, shows a higher frequency of hypoplasia in Narok South than in the Central Rift (difference statistically significant, $\chi^2 = 10.97$, $p = 0.001$) demonstrates that breed susceptibility to disease is not the only cause for the observed difference. This suggests that other environmental factors have to be identified, such as the effect of herd size and production systems in terms of risk for the introduction and transmission of disease, and resistance to rarefaction of resources. The caprine herds from the visited villages in the Central Rift all belong to mixed crop-livestock production systems, whereas the herding communities visited in Narok South District all practised extensive pastoralism and do not grow crops. Although herd size was not investigated, by definition it should be smaller in the mixed agriculture-farming system than in extensive pastoralist systems.

Differences between sheep and goat

Both feeding behaviour and resistance to disease might explain the observed difference in enamel hypoplasia frequency between sheep and goats. Preference for browsing by goats and predominant grazing by sheep, have been described in various semi-arid and tropical environments and in the study area (Balasse & Ambrose, 2005b). This difference in natural feeding behaviours implies that sheep would be more severely affected than goats by the rarefaction of grass during a drought episode.

The difference in enamel hypoplasia frequency between sheep and goats is more marked in the Central Rift than in Narok South. Several factors could account for the differences, including differential use of agricultural crop wastes, pathogens, restriction on mobility, overgrazing, and access to salt. Existence of mixed livestock-crop production systems in the Central Rift may be a factor. Livestock can be supplemented with by-products of agriculture. In this respect, goats appear more effective than sheep in using crops and plant food waste as fodder in the case of a drought. The communities visited in the Central Rift valley never mentioned the use of produced plants as fodder for caprines, although they were not specifically questioned on the subject. The two main crops raised on the Mau escarpment are maize, and potatoes at high elevation (Balasse & Ambrose 2005a). Because maize is a C4 plant, its consumption by goats would be detected in the carbon stable isotope composition ($\delta^{13}C$) of their tooth enamel. Because goats are predominantly browsers in these environments, they include a high proportion of C3 plants (most herbs and all trees and shrubs) in their diet. Although goats also include some graze and therefore C4 plants in their diet, among which wild grasses or cultivated maize cannot be distinguished using the $\delta^{13}C$ signature, a supplementation with maize in periods of drought would then raise the $\delta^{13}C$ in their enamel. Among the goat teeth included in the analysis, 22 had been previously isotopically analyzed (Balasse & Ambrose 2005b). This included five teeth formed over the 2000 drought period (Kat capra1 M3; Mar capra1 M2; Nai capra2 M2; Nai o/c2 M2 and Nda o/c1 M2). The $\delta^{13}C$ measured in these teeth is not higher than those measured in the other teeth. Therefore it is not possible to conclude that supplementation of goats with maize was practiced.

Overgrazing and environmental degradation appears to be occurring at a higher rate in the Central Rift than in Narok South (UNEP 2009). Because sheep are predominantly grazers, during the dry season they would suffer greater nutritional stress than goats, which are mixed feeders. Differences in mobility and access to pasture may also play a role in differences in hypoplasia frequency between sheep and goats in the Central Rift Valley. As noted above, mobility in the Central Rift is limited by fencing for small-scale and large farms and wildlife conservation areas. Options for herding sheep in appropriate dry season pastures may be greater in South Narok District.

Salt is considered essential for herd health and milk production (Dahl & Hjort 1976). Access to natural salt sources is more restricted in the Central Rift but there is no evidence for differential access to salt between sheep and goats. Moreover, salt may be more accessible in Narok, so this is unlikely to be a factor in the higher overall incidence of hypoplasias in this region.

Pathogen factors might also be considered to explain the difference in hypoplasia frequency between goats and sheep. Among the most prevalent infections in small ru-

minants in Kenya are respiratory and intestinal diseases. These affect both goats and sheep, but goats are reputed to be more resistant, and indigenous breeds are less susceptible than exogenous breeds, the latter being better represented in sheep than in goats. In the Central Rift the higher frequency of enamel hypoplasia in sheep compared to goat might therefore reflect the recurrence of nutritional stress and/or infectious diseases.

In the semi-arid environment of Narok South District, unexpectedly, the frequency of enamel hypoplasia is equally high in sheep and goats, suggesting that both species are affected to the same extent by semi-arid conditions and/or exposure to pathogens, although this might alternatively be explained by the small sample size.

The impact of the year 2000 drought on enamel hypoplasia

In the Central Rift as well as in Narok South District, the severe drought of 2000 does not seem to be distinguishable from other years in terms of frequency or severity of enamel hypoplasia (Table 5). Because of the small sample sizes, the difference between year 2000 and all other years taken together could be only tested for the frequency of hypoplasia in the Central Rift, where it was not significant (Chi- Squared test, $\chi^2 = 8.54$, $p = 0.07$). This might be partly explained by the imprecision in the attribution of ages, and therefore the estimation of the year of formation of the teeth. Moreover, even though the drought culminated in 2000, it began in 1999 and the herds had still not fully recovered in 2001. Some of the most affected animals might also have died or been slaughtered in anticipation of approaching fodder shortages by the herders, and consequently are not included in the assemblage.

Alternatively, nutritional or physiological stress occasioned by drought episodes may not be the main factor for the occurrence of enamel hypoplasia in the domestic caprine herds from southwest Kenya. Parasitic diseases, which are known to be a principal cause for mortality in Kenyan small ruminants (Kagira & Kanyaria 2001), might play a major role.

Conclusions

The high frequency of enamel hypoplasia observed in the domestic caprine herds from southwest Kenya most likely derives from environmental factors rather than stress linked to developmental physiology. The high frequency of enamel hypoplasia cannot be explained by nutritional or physiological stress linked to drought episodes alone, and infectious parasitic diseases are likely to play an important, if not preponderant role as a cause for these stress events. The higher frequency of enamel hypoplasia observed in sheep compared to goats may be explained both by different feeding behaviours and differences in resistance to disease between both species and between indigenous and exogenous breeds, the later being proportionally better represented in sheep. However, the higher frequency and severity of enamel hypoplasia observed in Narok South compared to the Central Rift is not explained by the relative proportion of each species nor by the relative proportion of exogenous breeds, and has to be seen as a reflection of the more fragile balance of the herding system in this arid climate compared to the more mesic climate of the Rift Valley. This suggests that other environmental factors have to be identified, including differences in herding practices. The effect of herd size and production systems in terms of risk for the introduction and transmission of disease, and resistance to rarefaction of resources needs to be considered. The caprine herds from the visited villages in the Central Rift all belong to mixed crop-livestock production systems whereas the herding communities visited in Narok South District all practised extensive pastoralism and do not grow crops. Although herd size was not investigated, by definition it should be smaller in the mixed agriculture-farming system than in extensive pastoralist systems. Future research should investigate more thoroughly differences in hypoplasia frequency and severity in exogenous and indigenous breeds, the effect of herd size, and long distance movement of herds between seasonal pastures.

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Appendix 1a

Frequency	CRV goat	CRV sheep	NAR goat	NAR sheep	CRV all	NAR all
CRV goat		X^2= 5.55; p=0.06	X^2= 10.97; p=0.001	*not tested*	*not tested*	*not tested*
CRV sheep	X^2= 5.55; p=0.06		*not tested*	X^2= 3.34; p=0.07	*not tested*	*not tested*
NAR goat	X^2= 10.97; p=0.001	*not tested*		X^2= 0.07; p=0.79	*not tested*	*not tested*
NAR sheep	*not tested*	X^2= 3.34; p=0.07	X^2= 0.07; p=0.79		*not tested*	*not tested*
CRV all	*not tested*	*not tested*	*not tested*	*not tested*		X^2= 13.27; p=0.001
NAR all	*not tested*	*not tested*	*not tested*	*not tested*	X^2= 13.27; p=0.001	
Severity	NAK goat	NAK sheep	NAR goat	NAR sheep	NAK all	NAR all
CRV goat		X^2= 3.16; p=0.08	X^2= 5.97; p=0.01	*not tested*	*not tested*	*not tested*
CRV sheep	X^2= 3.16; p=0.08		*not tested*	X^2= 6.84; p=0.08	*not tested*	*not tested*
NAR goat	X^2= 5.97; p=0.01	*not tested*		X^2= 3.25; p=0.20	*not tested*	*not tested*
NAR sheep	*not tested*	X^2= 6.84; p=0.08	X^2= 3.25; p=0.20		*not tested*	*not tested*
CRV all	*not tested*	*not tested*	*not tested*	*not tested*		
NAR all	*not tested*	*not tested*	*not tested*	*not tested*	X^2= 8.14; p=0.04	

Appendix 1b

Frequency	CRV ag	CRV mf	CRV sb	CRV ag+mf	CRV mf+sb
CRV ag		X^2= 3.67; p=0.06	X^2= 1.52; p=0.22		X^2= 2.49; p=0.11
CRV mf	X^2= 3.67; p=0.06		X^2=1.12; p=0.29		
CRV sb	X^2= 1.52; p=0.22	X^2=1.12; p=0.29		X^2=0.06; p=0.80	
CRV ag+mf			X^2=0.06; p=0.80		
CRV mf+sb	X^2= 2.49; p=0.11				
NAR all	*not tested*	*not tested*	X^2=9.19; p=0.01	*not tested*	*not tested*
Severity	CRV ag	CRV mf	CRV sb	CRV ag+mf	CRV mf+sb
CRV ag		X^2=1.16; p=0.28	X^2=3.68; p=0.06		X^2=3.18; p=0.08
CRV mf	X^2=1.16; p=0.28		X^2=0.53; p=0.47		
CRV sb	X^2=3.68; p=0.06	X^2=0.53; p=0.47		X^2=2.55; p=0.28	
CRV ag+mf			X^2=2.55; p=0.28		
CRV mf+sb	X^2=3.18; p=0.08				

Appendix 1: Results from statistical tests. CRV: Central Rift Valley; NAR: Narok South District; ag: high altitude grassland; mf: montane forest; sb: savanna bush.

Appendix 2

Central Rift	Tooth	1994	1995	1996	1997	1998	1999	2000	2001	2002
Ilk o/c 1	M1							0 1/1		
	M2							0	0	
Ilk o/c 2	M1						0 0			
	M2						0	0		
	M3							0	0	
Ilk o/c 3	M2						0	2/6		
	M3							1/4	1/1	
Ilk o/c 4	M2					0 1/4				
	M3					0	0			
Ilk o/c 5	M2			0	2/2					
	M3					0 1/1				
Ilk o/c 6	M1							0 1/1		
	M2								0	1/1
Ilk o/c 7	M1			0 0						
	M2			0	1/2					
	M3					0 4/6				
Ilk o/c 8	M2						0	1/1		
	M3								0	0
Ilk o/c 9	M1						0 1/1			
	M2							0	1/2	
Ilk o/c 10	M1						0 2/2			
	M2							0	1/1	
Mog o/c 1	M1						0 3/5			
	M2							2/2	2/1	
	M3								0	0
Mog o/c 2	M1						0 2/2			
	M2							0	0	
	M3								1/2	0
Mog o/c 3	M1				0 0					
	M2					0 1/2				
	M3						0 1/3			
Mog o/c4	M1					0 1/3				
	M2						1/2 2/4			
	M3							0 2/3		
Mog o/c5	M1					0 2/2				
	M2						0 4/6			
	M3							0 2/4		
Nai ovis 1	M2					0 1/1				
	M3						0 4/10			
Nai ovis 2	M2					0 3/5				
	M3						0 2/3			
Nai ovis 3	M2						0 0			
Nai capra 1	M2					0 2/2				
	M3						0 1/2			
Nai capra 2	M1						0 1/1			
	M2							0	0	
	M3								1/3	0
Nai capra 3	M1								0	2/2
	M2									0 0

Appendix 2 (*continued*)

Central Rift	Tooth	1994	1995	1996	1997	1998	1999	2000	2001	2002
Nai o/c 1	M2		0	0						
	M3			0	0					
Nai o/c 2	M1						0 0			
	M2						0	0		
Nai o/c 3	M3				0	3/5				
Nai o/c 4	M3			0	0					
Nai o/c 5	M2	0	3/8							
	M3		0	3/6						
Nai o/c 6	M2					0 3/5				
	M3						1/2 1/1			
Nai o/c 7	M2	0	1/0							
	M3		0	2/3						
Nai o/c 8	M1			0 2/4						
Nai o/c 9	M2				0	1/3				
Kat capra 1	M2					0	0			
	M3						0	1/0		
Kat o/c 1	M1			0 2/1						
	M2			0	1/4					
	M3				0	2/0				
Kat o/c 2	M1							0 2/4		
Kat o/c 3	M1						0 1/1			
	M2							0	0	
Mar ovis 1	M1						0 1/1			
Mar capra 1	M1						0 1/1			
	M2							0	0	
Mar o/c 1	M1		0 1/3							
	M2		0	2/4						
	M3			0	3/6					
Nda ovis 1	M1							0 0		
Nda o/c 1	M1						0 1/1			
	M2							0	1/2	
	M3								1/2	0
Nda o/c 2	M1						0 0			

Appendix 2 (*continued*)

Narok South	Tooth	1994	1995	1996	1997	1998	1999	2000	2001	2002
Oloi o/c 1	M1			0 0						
	M2			0	2/1					
Oloi o/c 2	M1						1/1 2/5			
	M2						2/5	2/5		
	M3							2/8	1/3	
Oloi o/c 3	M1								0 2/2	
	M2								0	0
Ole ovis 1	M2							0	2/2	
Ole capra 1	M1							0 0		
	M2							0	0	
Ole o/c 1	M1				0 3/9					
	M2				0	1/1				

Appendix 2 (*continued*)

Narok South	Tooth	1994	1995	1996	1997	1998	1999	2000	2001	2002
	M3					0	0			
Ole o/c 2	M2			0	1/2					
	M3				0	2/3				
Enk capra 1	M1						0 2/2			
	M2						0	3/6		
Enk capra 2	M1							0 0		
	M2							1/4	2/4	
Enk capra 3	M1							0 1/3		
	M2							0	3/2	
Enk capra 4	M1						0 4/6			
	M2						0	4/10		
	M3							1/2	4/16	
Enk o/c 1	M1					0 3/6				
	M2					0	3/4			
	M3						0	5/11		
Enk o/c 2	M1								1/2 1/4	
Enk o/c 3	M3				0	3/7				
Enk o/c 4	M1					0 0				
	M2					0	2/4			
Enk o/c 5	M1					0 2/2				
	M2					0	4/7			
	M3						0	1/3		

Appendix 2: Estimated period of formation of the sheep and goat molars included in the analysis. (1/2): Frequency/severity of hypoplasia in each half crown.

Appendix 2: Raw data from Orkney

NB: 'Height' refers to the height of the tooth crown and where a tooth crown is recorded as incomplete the location of enamel hypoplasia is recorded from the occlusal tip of the tooth following the methodology discussed in Chapter 4.

North Ronaldsay First Molars in Payne age category C

Sample code	Age group	crown complete	L / R	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.2a	C	y	R	31.66	7	19.81	none	line	1
						8.04	9.73	shift	
						4.97	none	line	1
84.12a	C	y	L	23.46	8	19.94	none	line	1
						11.75	12.31	depression	
						5.07	4.94	line	1
84.7b	C	y	R	24.39	8	20.75	21.59	line	1
						9.18	none	shift	
84.47a	C	y	L	23.71	7	8.44	7.82	shift	
84.5b	c	y	R	26.58	6	7.53	7.15	depression	
84.69	c	y	l	26.41	1	19.17	none	line	1
						none	11.88	depression	
						11.06	10.2	line	1
84.7a	c	y	r	25.1	7	11.89	none	line	1
						7.19	none	shift/depression	
84.82	c	y	r	25.54	3	18.76	20.66	line	1
						14.02	13.8	line	1
						none	10.96	line	1
84.12	c	y	r	24.76	4	13.58	19.09	line	2
						4.74	none	large pit	
84.71	c	y	r	25.86	7	11.22	12.9	line	1
84.98	c	y	l	23.32	6	7.56	8.54	depression	
84.59	c	y	l	25.17	6	13.09	none	line	1
						7.95	11.16	shift	
						3.72	4.69	line	1
84.57	c	y	r	25.6	6	9.54	11.51	depression	
						3.73	none	line	1
84.2	c	y	r	25.03	6	19.21	21.01	line	1
						7.39	none	pits/depression	
84.31	c	y	r	22.76	7	16.75	19.19	line	1
						none	4.34	line	1
84.106	c	y	r	22.24	7	7.54	10.99	depression	
84.81	c	y	r	26.52	3	20.25	19.29	line	1
						7.87	8.99	line	2
84.62	c	y	l	24.7	6	19.01	19.93	line	2
						6.83	7.60	shift	
84.53	c	y	l	26.27	7	8.57	9.03	shift	
84.65	c	n	l	27.55	3	none	8.80	line	1
						12.49	none	line	1
83.8	c	y	r	25.63	6	18.27	20.45	line	1
						6.96	8.77	depression	
84.58	c	y	l	25.10	5	none	none		
84.83	c	n	l		4	6.92	7.41	line	1
						13.08	13.53	line	1
84.99	c	n	l		3	8.65	none	line	1

North Ronaldsay First Molars in Payne age category D

Sample code	Age group	L/R	crown complete	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.66	D	r	y	21.42	7	8.59	10.53	shift	
84.38	D	L	y	32.82	8	9.67	11.92	shift	
						none	6.85	line	1
						3.2	3.75	line	1
83.9	d	r	y	23.3	7	10.98	11.83	pression/ line	
						8.62	none	line	1
						4.25	5.39	line	1
84.13	d	l	y	21.8	8	18.87	21.07	line	1
						7.5	8.81	depression	
						2.75	3.5	line	1
						none	1.25	line	1
84.16a	d	r	y	20.43	8	8.48	10.01	depression	
						5.98	6.53	line	1
						2.95	none	line	1
84.27a	d	r	y	20.81	8	8.65	9.67	shift	
						4.12	4.9	line	1
83.2	d	r	y	20.05	8	7.58	none	depression	
84.76	d	r	y	17.79	8	none	none		
84.9	d	l	y	23.38	7	none	none		
84.72	d	r	y	21.81	7	13.39	14.61	depression	
						8.13	8.62	depression	
						none	4.72	depression	
84.122	d	l	y	20.79	8	6	6.84	depression	
84.3	d	r	y	20.98	8	7.41	9.36	shift	
						3.97	4.02	depression	
84.3	d	l	y	22.3	8	17.45	17	line	1
						6.68	5.73	depression	
						3.58	3.07	depression	
84.107	d	l	y	21.44	7	10.83	12.64	depression	
						4.13	2.8	line	2
84.105	d	l	y	21.36	8	none	none		
84.83	d	l	y	19.98	8	9.23	10.86	depression	
						none	5.06	line	1
84.101	d	r	y	23.09	7	none	none		
84.15	d	r	y	16.13	8	none	11.05	pit	
						none	9.33	pit	
84.8	d	r	y	20.49	7	8.32	5.41	depression	
84.109	d	l	y	21.76	7	16.25	18.98	line	1
						8.72	10.04	depression	
84.28	d	r	y	23.31	6	7.35	7.86	depression	

North Ronaldsay First Molars in Payne age category E

Sample code	Age group	crown complete	L / R	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.86	E	y	L	18.07	8	cementum	cementum		
84.121	e	y	r	20.15	8	7.92	9.31	shift	
						2.66	none	depression	
84.25a	e	y	r	20.27	8	8.63	9.13	shift	
84.29	e	y	r	18.25	8	cementum	cementum		
84.63	e	y	l	20.11	8	cementum	cementum		
84.68	e	y	r	17.4	8	6.03	6.96	line	1
						none	4.4	line	1
84.14b	e	y	l	18.71	8	9.14	9.14	line	1
84.64	e	y	l	missing	--	--	--	--	--
84.39	e	y	l	23.31	7	none	none		
84.26	e	y	r	19.7	8	cementum	cementum		
83.30	e	y	l	21.98	8	12.19	15.83	depression	
						7.32	8.22	depression	
						4.69	5.02	depression	
84.77	e	y	l	19.6	8	cementum	cementum		
84.11	e	y	l	20.02	8	none	7.18	line	1
						none	3.9	line	1
83.10	e	y	r	18.64	8	10.49	12.93	depression	
84.54	e	y	r	17.77	8	cementum	cementum		
84.78	e	y	l	20	8	cementum	cementum		

North Ronaldsay First Molars in Payne age category F

Sample code	Age group	crown complete	L / R	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.126	f	Y	r	11.42	8	4.2	5.8	large pit A cusp	
								pit n depression p cusp	
83.13	f	Y	r	15.86	8	8.59	none	shift	
84.1b	f	Y	l	16.46	8	cementum	cementum	--	
84.67	f	Y	l	14.44	8	cementum	cementum	--	
84.46b	f	Y	l	14.44	8	cementum	cementum	--	
84.6	f	Y	l	12.93	8	cementum	cementum		
83.5	f	Y	r	18.68	8	8.43	9.15	shift / pit	
						5.32	4.14	line	2
84.45a	f	Y	r	17.1	8	none	none		
83.12	F	Y	L	19.16	8	cementum	cementum		
84.108	f	Y	l	14.05	8	cementum	cementum		
84.52	f	Y	r	missing					
84.110	f	Y	l	14.68	8	none	none		
84.88	f	Y	l	18.32	8	cementum	cementum		
84.49	f	Y	r	14.89	8	cementum	cementum		
84.49	f	Y	l	19.2	8	none	none		
84.75	f	Y	r	15.18	8	cementum	cementum		
84.85	f	Y	r	19.46	8	cementum	cementum		
83.14	f	Y	l	20.73	8	9.65	9.73	line/depression	1
83.16	f	Y	l	15.81	8	8.57	10.05	line	2
						--	6.12	pit	
84.61	f	Y	r	15.72	8	7.47	10.53	pit/line	2
83.4	f	Y	r	20.16	8	9.12	7.61	depression	
84.4	f	Y	l	18.93	8	cementum	cementum		
84.93	f	Y	r	18.41	8	8.72	8.43	depression	

North Ronaldsay Second Molars in Payne age category C

Sample code	Age group	crown complete	L / R	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.2a	C	N	R	--	1	--	--	--	--
84.12a	C	N	L	--	1	12.96	10.29	line	1
84.7b	C	N	R	--	1	12.85	10.22	line	3
84.47a	C	N	L	--	1	--	--	--	--
84.5b	c	n	R	--	1	--	--	--	--
84.69	c	N	1	--	1	--	--	--	--
84.7a	c	n	r	--	1	--	--	--	--
84.82	c	n	r	--	1	--	--	--	--
84.12	c	n	r	--	1	--	--	--	--
84.71	c	n	r	--	1	--	--	--	--
84.98	c	n	1	--	1	12.24	9.27	line	1
84.59	c	n	1	--	1	--	--	--	--
84.57	c	n	r	--	1	--	--	--	--
84.2	c	n	r	--	1	--	--	--	--
84.31	c	n	r	--	2	--	--	--	--
84.106	c	n	r	--	1	--	--	--	--
84.81	c	n	r	--	1	--	--	--	--
84.62	c	n	1	--	1	--	--	--	--
84.53	c	n	1	--	1	--	--	--	--
84.65	c	n	1	--	unerrupted	--	--	--	--
83.8	c	n	r	--	1	--	--	--	--
84.58	c	n	1	--	unerrupted	--	--	--	--
84.83	c	n	1	--	unerrupted	--	--	--	--
84.99	c	missing	1	--	--	--	--	--	--

North Ronaldsay Second Molars in Payne age category D

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.66	D	r	n	--	4	none	none		
84.38	D	L	N	--	5	none	none		
83.9	d	r	n	--	3	none	none		
84.13	d	l	y	33.93	4	16.74	18.24	line through pits	
						20.57-16.44	23.03-16.02	pits (top-botton)	
84.16a	d	r	y	29.72	6	7.58	none	line	1
						4.39	none	line	1
						none	2.13	line	1
84.125	d	l	y	27.51	7	5.37 -2.40	5.86 - 2.63	hypomineralised	
						5.32	5.8	line	2
						3.57	4.59	line	2
						2.42	3.33	line	3
84.27a	d	r	y	32.52	5	7.56	10.19	depression	
83.2	d	r	n		4	none	none		
84.76	d	r	y	28.33	7	17.47	none	line	1
						6.99	8.42	depression	
						0.84	2.52	line	1
						none	1.31	line	2
84.9	d	l	y	32.1	5	none	25.14	pit	
						7.29	8.64	depression	
						none	1.93	pit	
84.72	d	r	n		3	none	none		
84.122	d	l	y	31.15	4	none	none		
84.3	d	r	y	32.82	4	none	none		
84.3	d	l	y	32.4	4	none	none		
84.107	d	l	y	31.99	6	17.29	17.3	line	1
84.105	d	l	n		2	none	none		
84.83	d	l	y	30.34	5	13.93	15.26	line	1
						7.28	none	line	1
						4.03	none	line	1
						none	2.04	depression	
84.101	d	r	y	31.79	5	10.6	none	depression	
84.15	d	r	y	25.9	7	none	13.31	pits	
						7.21	8.01	depression	
						4.01	4.43	line	3
						0.91	1.81	line	2
						none	0.66	line	2
84.8	d	r	y	29.83	4	none	none		
84.109	d	l	n		2	none	none		
84.28	d	r	n		3	none	none		

North Ronaldsay Second Molars in Payne age category E

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.86	E	L	y	28.09	8	none	5.58	line	1
							3.72	line	1
84.121	e	r	y	29.86	8	11.67	12.86	line	1
84.25a	e	r	y	29.09	7	4.98	none	pits	
						2.75	3.32	pits	
84.29	e	r	y	27.54	8	9.99	none	depression	
						5.66	5.08	depression	
84.63	e	l	y	29.02	6	11.31	10.37	depression	
						6.52	5.53	line	1
						2.68	none	line	1
84.68	e	r	y	25.18	7	none	17.51	line	1
						11.12	11.76	line	1
						none	8.18	line	1
84.14b	e	l	y	26.88	8	2.92	3.64	depression	
						none	2.34	line	1
84.64	e	l	y	27.51	7	3.25	3.9	line	1
						2.42	2.04	line	1
84.39	e	l	y	32.49	6	none	11.51	depression	
						none	2.67	line	1
84.26	e	r	y	28.7	8	cementum	cementum		
83.30	e	l	y	31.41	6	11.78	12.12	line	1
						8.42	9.97	line	1
						none	1.66	line	1
84.77	e	l	y	28.25	7	8.41	9.35	depression	
84.11	e		y	27.61	7	3.34	4.14	line	1
						none	1.72	line	2
83.10	e	r	y	28.54	7	9.01	9.58	line	1
84.54	e	r	y	28.7	7	cementum	cementum		
84.78	e	l	y	31.12	7	8.58	10.47	depression	
						4.85	5.64	depression	

North Ronaldsay Second Molars in Payne age category F

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
84.126	f	r	y	23.5	8	4.85	4.35	depression	
						--	1.29	line	2
83.13	f	r	y	24.36	8	cementum	cementum	--	
84.1b	f	l	y	27.33	8	10.29	12.34	depression	
						none	3.08	depression	
84.67	f	l	y	23.92	8	8.51	10.43	depression	
						5.27	5.79	line	1
						none	4.04	line	1
84.46b	f	l	y	25.35	8	none	n		
84.6	f	l	y	20.86	8	cementum	cementum		
83.5	f	r	y	27.71	8	11.86	13.56	depression	
						none	9.35	line	1
84.45a	f	r	y	27.03	8	none	n	n	
83.12	F	L	Y	29.98	7	10.4	12.24	line	1
						6.11	6.13	line	1
84.108	f	l	y	24.73	8	4.42	5.25	line	1
						1.36	1.77	line	2
84.52	f	r	y	25.6	7	6.51	6.73	line	1
						4.66	4.35	line	1
84.110	f	l	y	23.59	8	--	1.95	line	1
						--	0.67	line	1
84.88	f	l	y	26.57	8	cementum	cementum		
84.49	f	r	y	23.01	8	2.29	1.9	line	1
84.49	f	l	y	29.08	7	none	none		
84.75	f	r	y	25.37	8	9.71	--	depression	
						1.72	2.81	line	1
						--	0.81	line	1
84.85	f	r	y	26.23	8	cementum	cementum		
83.14	f	l	y	30.59	7	10.43	11.5	depression	
						3.08	3.93	line	1
						1.64	2.1	line	1
83.16	f	l	y	22.73	8	5.5	5.19	line	1
						2.2	2	line	1
84.61	f	r	y	24.87	8	none	none		
83.4	f	r	y	30.12	7	none	none		
84.4	f	l	y	26.65	8	none	none		
84.93	f	r	y	26.82	8	0.42	1.48	line	1

North Ronaldsay Third Molars in Payne age category D

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
84.66	D	r	not developed							
84.38	D	L	not developed							
83.9	d	r	not developed							
84.13	d	l	not complete		unerrupted	none	none	none		
84.16a	d	r	damaged							
84.125	d	l	not developed							
84.27a	d	r	not developed							
83.2	d	r	not developed							
84.76	d	r	not complete		1	9.7	6.35	none	line	1
						15.74	13.23	none	line	1
84.9	d	l	not complete		1	none	none	none		
84.72	d	r	not developed							
84.122	d	l	not complete		unerrupted	none	none	none		
84.3	d	r	not complete		unerrupted	none	none	none		
84.3	d	l	not complete		unerrupted					
84.107	d	l	missing							
84.105	d	l	not developed							
84.83	d	l	not complete		1	none	none	none		
84.101	d	r	not complete			none	none	none		
84.15	d	r	not complete		1	none	none	none		
84.8	d	r	not complete		1	none	none	none		
84.109	d	l	not developed							
84.28	d	r	not developed							

North Ronaldsay Third Molars in Payne age category E

Sample code	Age group	L / R	wn compl	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
84.86	E	L	y	32.16	4	6.14	7.93	9.91	line	1
						3.94	5.23	7.25	line	1
						none	3.23	4.1	line	2
						none	1.78	2.31	line	1
84.121	e	r	y	36.07	3	none	none	none		
84.25a	e	r	y	32.44	4	6.53	none	6.09	pits	
						2.39	none	none	pits	
84.29	e	r	y	33.35	4	25.33-20.98	25.75	none	fine spaced out pits	
						6.05	6.77	8.25	line	1
						none	2.04	3.05	line	2
84.63	e	l	y	33.11	2	17.75	20.52	none	lines	1
						9.47	11.24	8.4	lines	1
84.68	e	r	y	30.67	4	9.73	11.65	none	line	1
						8.1	9.45	9.45	line	1
						5.89	7.24	5.19	line	1
						3.77	none	2.12	line	1
84.14b	e	l	y	33	4	19.05	none	none	line	1
						none	none	10.29	line	1
						none	none	8.24	line	1
84.64	e	l	y	32.57	4	10.12	none	none	line	1
						1.29	1.11	1.99	line	3
84.39	e	l	no		2	none	none	none		
84.26	e	r	y	32.35	4	7.37	none	none	pits	
						4.69	1.82	none	pits / lines	
						2.43	0.54	1.24	line	1
83.30	e	l	y	34.4	2	none	none	none		
84.77	e	l	y	33.18	2	17.11	19.69	none	line	1
						13.2	15.61	none	line	1
						9.71	11.37	9.16	line	1
						6.4	6.94	7.07	line	1
84.11	e	l	y	32.16	3	1.59	3.93	4.9	line	1
						none	2.6	3.07	line	1
83.10	e	r	y	33.75	3	none	none	none		
84.54	e	r	y	33.69	4	3.76	3.06	2.44	line	2
84.78	e	l	y	34.19	4	7.7	10.02	missing	line	1
						3.37	3.31	missing	line	2

North Ronaldsay Third Molars in Payne age category F

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
84.126	f	r	y	30.11	9	7.92	11.45	15.23	line	1
						4.36	6.05	10.45	line	3
						2.63	5.41	7.19	line	3
						none	2.65	4.13	line	3
						none	1.25	2.47	line	2
						none	none	1.03	line	1
83.13	f	r	y	31.14	9	4.47	4.47	4.47	line	2
						none	2.24	1.29	line	1
84.1b	f	l	y	31.21	9	3.37	none	none	line	1
84.67	f	l	y	30.76	9	5.72	6.64	8.24	line	1
84.6	f	l	y	25.36	9	cementum	cementum	cementum		
83.5	f	r	y	31.84	9	6.18	9.55	10.41	depression	
84.45a	f	r	y	31.42	9	cementum	cementum	cementum		
83.12	F	L	Y	33.12	4	none	none	none		
84.108	f	l	y	29.75	8	8.24	9.96	12.52	line	1
						6.19 - 3.84	6.6 - 4.76	8.79 - 7.03	top - bottom of wide line	4
						2.46	3.53	5.47	line	1
						1.81	2.12	5.18	line	3
84.52	f	r	y	31.44	5	7.99	8.44	--	line	1
						4.98	--	--	line	1
						1.71	1.79	2.7	line	2
						--	0.62	0.8	line	1
84.110	f	l	y	28.18	8	--	1.79	1.66	depression	
84.88	f	l	y	30.55	9	--	1.81	2.69	depression	
84.49	f	r	y	29.03	8	7.31	8.42	--	line	1
						5.13	5.17	7.65	line	1
						4	4.26	5.59	line	2
						--	--	1.21	line	1
84.49	f	l	y	33.15	6	3.59	5.96	3.69	line	1
84.75	f	r	y	31.67	9	8.4	--	--		
						4.89	5.69	7.82	depression	
						1.62	1.35	1.4	line	1
84.85	f	r	y	30.79	8	8.21	--	--	depression	
						--	2.45	4.21	line	1
						--	0.89	1.3	line	1
83.14	f	l	y	35.28	7	--	--	9.63	depression	
83.16	f	l	y	27.37	9	7.44	7.66	8.42	line	1
						--	5.26	5.96	line	1
						--	2.67	3.16	line	1
						--	1.6	1.84	line	1
84.61	f	r	y	30.54	9	none	none	none		
83.4	f	r	y	35.02	8	--	--	4.94	pit	
84.4	f	l	y	30.91	9	cementum	cementum	cementum		
84.93	f	r	y	31.33	9	--	1.16	2.08	depression	

Hoy First Molars

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
546	c	r	y	24.66	6	--	--		
548	c	l	y	22.69	8	--	--		
2893	c	r	y	23.63	8	9.04	10.12	depression	
541	c	R	N	--	6	--	--		
2867	C	R	Y	24.56	7	--	--		
2912	D	R	Y	24.44	8	9.13	--	depression	
558	D	R	Y	20.14	8	--	--		
2868	d	r	y	20.1	8	--			
2892	d	r	y	17.64	8	--	10.81	depression	
2938	d	r	y	22.42	7	--			
549	d	r	y	16.97	8	8.44	4.98	line	1
						--	1.95		1
543	d	r	y	18.94	8	--			
555	d	r	y	26.88	7	--			
800	E	l	y	19.3	8	--	15.41	pit	--
						--	10.75	pits	--
669	e	l	y	20.03	8	calculus	calculus		
560	e	l	y	18.35	8	--	--		
550	e	l	y	19.79	8	12.76	--	line	1
3217	e	l	y	18.37	8	--			
545	e	l	y	23.58	8	7.87	7.88	depression	
552	e	l	y	18.31	8	--			
659	e	l	y	18.63	8	8.51	--	line	1
						--	2.76	line	1
2944	e	l	y	18.58	8	9.5	--	line	1
						6.16	6.38	depression	
542	e	l	y	17.21	8	--	--		
2866	e	l	y	20.42	8	--	--		
2913	e	l	y	18.61	8	--	--		
547	f	l	y	14.88	8	--	--		
667	f	l	y	10.65	10	--	--		
660	f	l	y	14.89	8	--	--		
556	f	l	y	16.65	8	3.97	5.4	line	1
2914	f	l	y	16.26	8	--	--		
2894	F	L	y	20.22	8	3.85	3.25	line	1
514	f	l	y	13.17	8	cal	cal		
553	f	l	y	10.86	11	--	--		
508	f/g	l	y	broken	broken	--	--		

Hoy Second Molars

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
546	c	r	n	--	undeveloped				
548	c	l	n	--	undeveloped				
2893	c	r	n	--	undeveloped				
541	c	R	N	--	undeveloped				
2867	C	R	N	--	undeveloped				
2912	D	R	N	--	3				
558	D	R	Y	34.05	6	14.47	13.33	line	1
						9.44	10.29	line	1
2868	d	r	y	30.15	6	--			
2892	d	r	y	29.79	8	--	7.77	line	1
2938	d	r	y	32.16	3	--			
549	d	r	y	28.65	6	7.62	16.67	depression	
						11.68	12.73	line	1
543	d	r	y	29.52	6	--			
555	d	r	y	35.01	2	10.81	11.64	line	1
800	E	l	y	29.42	6	11.75	11.77	depression	
669	e	l	y	28.93	8	10.4	--	line	1
						--	12.49 -7.23	large pit	
560	e	l	y	28.33	8		--	--	
550	e	l	y	30.07	8	9.04	--	depression	
3217	e	l	y	27.62	6	14.44	15.45	line	1
						9.01	9.68	line	1
						5.78	6	line	1
545	e	l	y	35.77	7	14.42	--	pit	
						12.09	--	line	1
						6.86	--	line	1
552	e	l	y	28.04	8	16.71	18.78	depression	
						10.28	12.61	depression	
						5.81	6.8	depression	
659	e	l	y	26.44	8	10.16	10.11	line	1
						9.64	7.57	line	1
2944	e	l	y	28.27	7	--	7.57	depression	
542	e	l	y	28.49	7	12.24	--	depression	
2866	e	l	y	29.29	7	14.64	15.53	pits	
						12.88	13.6	line / pits	2
2913	e	l	y	29.79	7	--	--		
547	f	l	y	24.22	8	--	--		
667	f	l	y	21.17	8	2.02	--	pit	
660	f	l	y	23.4	8	9.52	10.27	depression	
						6.36	6.87	line	1
556	f	l	y	28.11	8	--	--		
2914	f	l	y	24.44	8	6.67	7.65	line	1
						--	1.71	line	2
2894	F	L	y	28.29	6	14.35	13.43	line	1
						9.26	9.39	line	1
						5.45	5.02	line	1
						2.57	2.36	line	1
514	f	l	y	24.02	8	14.82	16.65	line	1
						8.9	9.43	depression	
553	f	l	y	22.06	8	11.78	11.53	depression	
						6.54	6.87	line	1
508	f/g	l	y	19.94	8	3.6	4.23	depression	

Hoy Third Molars

Sample code	Age group	L / R	crown complete	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
546	c	r	not developed							
548	c	l	not developed							
2893	c	r	not developed							
541	c	R	not developed							
2867	C	R	not developed							
2912	D	R	not developed							
558	D	R	Incomlete							
2868	d	r	Incomlete							
2892	d	r	Incomlete							
2938	d	r	Incomlete							
549	d	r	Incomlete							
543	d	r	Incomlete							
555	d	r	not developed							
800	E	l	y	34.41	7	--				
669	e	l	y	34.14	2	6.99	7.77	8.85	pits	
560	e	l	y	34.63	4	--	--	--		
550	e	l	y	36.12	5	16.64	20.93	20.96	line	1
						14.21	16.61	17.03	line	1
						10.86 - REJ	10.87 - REJ	12.79- - REJ	large aplastic area -	4
3217	e	l	y	33.65	3	18.03	--	--	line	1
						--	9.96	10.37	depression	
545	e	l	Incomlete							
552	e	l	Incomlete							
659	e	l	y	35.42	4	13.23	14.36	14.88	line	1
						7.66	5.5	9.24	depression	
2944	e	l	y	34.62	5	9.58	10.86	12.1	line	2
542	e	l	y	32.95	3	15.61	--	--	line	1
						11.56	14.01		line	1
						6.9	8.31	9.41	depression	
2866	e	l	y	35.33	3	11.28	11.36	11.47	depression	
2913	e	l	incomplete	--	2	15.08	12.29	9.21	line	1
						19.16	16.74	13.28	line	1
547	f	l	y	30.2	9	--	--	--		
667	f	l	y	26.89	8	--	--	3.86	depression	
660	f	l	y	30.26	6	10.42	10.02	--	line	1
						5.85	7.11	8.5	line	1
						2.07	3.07	4.71	line	2
556	f	l	y	34.71	7	--	--	--		
2914	f	l	y	29.7	7	15.83 - REJ	17.66- REJ	17.03- REJ	large aplastic area	4
2894	F	L	y	34.07	6	8.29	10.7	12.58	depression	
514	f	l	y	28.29	8	cal	cal	cal		
553	f	l	y	30.18	10	13.77	14.61	--	line	1
						7.19	6.4	5.09	line	1
508	f/g	l	y	25.65	10	11.26	13.96	--	line	1
						--	--	10.72	line	1
						5.79	6.65	7.61	line	1
						2.78	3.88	5.79	depression	

Skara Brae First and Second Molars

Sample code	Context	L / R	crown complete	Height	wear stage	M1 / M2?	A Cusp hypo	P Cusp hypo	type	severity
1	102	r	y	24.94	7	?	--	--		
2	102	r	y	35.89	3	?	--	--		
3	102	r	y	24.71	8	?	--	15.14	line	1
4	102	r	y	35.78	4	?	--	--		
5	102	r	n	28.5	3	?				
6	102	r	y	19.73	8	m1	8.45	7.24	depression	
7	102	r	y	31.85	6	m2	21.44	22.23	depression	
							--	1.39	line	1
8	102	r	y	25.84	6	?	7.43	7.06	pits	
							3.37	4.29	line	1
							1.86	3.28	line	1
24	102	l	y	30.98	6	?	--	--		
25	102	l	y	18.93	8	?	8.45	12.62	depression	
							5.06	8.17	line	1
34	102	r	y	11.66	8	?	--	--		
35	102	r	y	24.15	8	?	--	--		
39	102	r	y	16.69	8	?	6.46	6.63	depression	
40	102	r	n	25.83	2	?	--	--		
41	102	r	n	27.12	1	?	--	--		
42	102	l	n	21	1	?	--	--		
46	102	l	n	18.32	1	?	--	--		
47	102	l	n	21.9	1	?				
63	157	l	y	20.61	8	m2	--	--		
64	157	l	y	15.34	8	m1	--	--		
65	157	r	y	35.94	6	?	--	--		
66	157	r	y	22.2	8	?	--	--		
67	157	r	y	24.67	6	?	--	--		
68	157	r	y	16.38	8	?	--	--		
69	157	l	y	25.26	2	?	--	--		
70	157	r	y	35.85	2	?	--	--		
83	168	l	y	22.3	7	m1	--	--		
84	168	r	y	23.61	8	m1	--	--		
86	102	l	y	24.77	8	?	13.23	14.6	depression	
							7.73	9.36	depression	
							4	4.81	line	3
							1.9	--	line	1
87	102	r	y	24.66	8	?	--	--		
88	102	l	y	29.51	6	?	--	11.2	depression	
89	102	l	n	28.14	4	?	--	12.76	depression	
90	102	r	y	30.72	6	?	--	--		
91	102	l	y	35.06	4	?	7.02	--	depression	
							19.99	20.44	ne / depressio	3
92	102	r	y	22.68	8	?	9.5	--	depression	
93	102	r	y	24.91	6	?	--	--		
94	102	r	y	25.5	8	m2	7.58	--	pits	
96	102	l	y	18.59	8	m1	10.34	11.93	line	1
97	102	l	y	31.18	6	m2	11.58	14.9	depression	
							--	1.93	line	1
98	102	r	n	24	1	?	--	--		
99	102	l	n	20	1	?	--	--		
100	102	r	n	21.5	1	?	--	--		
137	102	r	y	32.45	6	?	--	--		
138	102	r	y	26.84	6	?	--	--		
139	102	l	y	25.15	6	?	--	--		
140	102	r	y	27.07	4	m1	--	--		
141	102	r	y	18.68	8	m1	15.52	17.51	depression	
142	102	r	n	21	1	?	--	--		
143	102	l	n	19	1	?	--	--		
144	102	l	y	26.04	8	?	--	--		
145	102	l	y	24.99	7	?	11.91	11.02	pit/depression	
							7.05	6.16	depression	
146	102	l	y	23.66	6	?	--	--		
147	102	r	n	25	1	?	--	--		
148	102	l	n	22.5	1	?	--	--		
151	102	l	y	26.49	3	?	--	--		
152	102	l	y	27.8	4	?	--	--		
158	102	r	y	26.62	3	?	--	--		
159	102	r	n	28	1	?	--	--		
160	102	L	y	23.92	8	?	7.2	6.86	depression	
161	102	l	y	26.86	6	m1	--	--		
162	102	r	y	23.31	5+	?	--	15.01	depression	
163	102	r	n	28.93	2	?	--	--		
164	102	r	y	27.95	4	?	--	--		
165	102	l	n	29.5	3	?	--	--		
180	102	l	n	16.5	1	?	--	--		
187	162	l	n	29.17	6	?	--	--		
190	154	r	y	25.48	8	m1	13.21	15.62	depression	
191	154	r	y	35.98	3	m2	7.78	7.3	depression	
192	213	r	y	30.31	7	m2	16.47	15.41	pit/depression	
							11.01	9.4	depression	
193		l	y	34.65	6	m2	9.62	12.22	pit/depression	
							6.14	6.29	depression	
194	213	r	y	19.75	8	?	7.45	8.95	line	2
202	213	l	y	22.89	8	?	--	1.15	line	2
203	213	l	y	23.68	8	?	--	--		
204	213	r	n	27	3	?	--	--		
209	213	l	n	30.03	2	?	--	--		
210	213	l	y	24.8	8	?	--	--		
211	213	r	y	24.21	8	?	--	--		

Skara Brae Third Molars

Sample code	Context	L / R	crown complete	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
9	102	r	y	15.03	10	5.62	7	--	line	2
26	102	l	y	37.46	2	7.06	4.61	4.46	depression	
27	102	l	n	29.91	1					
36	102	r	n	37.43	2					
48	102	l	n	35.15	1					
71	157	l	n	32.00	1	27	25	broken	depression	
72	157	r	n	28.00	1					
95	102	r	y	29.51	6	--	0.98	--	line	2
101	102	l	y	36.13	3	--	--	--		
102	102	l	y	29.14	8	7.08	6.72	7.57	depression	
103	102	r	n	29.50	1	--	--	--		
188	162	l	y	31.46	6	--	--	--		
200	213	r	y	37.92	2	5.4	5.35	7.22	depression	

Appendix 3: Raw data from Kenyan Archaeological Sites

NB: 'Height' refers to the height of the tooth crown and where a tooth crown is recorded as incomplete the location of enamel hypoplasia is recorded from the occlusal tip of the tooth following the methodology discussed in Chapter 4.

Lemek North East Third Molars

Sample code	SQ	Spit	Species	L / R	crown complete	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	Type	severity
18	H6	0-10	ovis	r	y	21.01	10	10.22	12.43	14.76	line	2
								5.84	6.95	9.16	line	2
								3.41	4.34	5.85	line	2
								1.15	1.61	--	line	1
27	F5	B	capra	r	n		3	--	14.21	13.37	depression	
24	F6	B	capra	l	y	25.48	10	3.55	3.62	2.44	line	2
								1.96	2.52	--	line	2
17	I6	B	capra	l	y	26.67	10	13.53	13.3	16.3	line	2
								3.86	4.35	7.42	line	2
								1.49	1.64	3.65	line	2
										2.55	line	2
31	I6	B	O?	r	y	15.03	13	3.61	3.62	4.5	line	2
32	I6	B	capra	r	y	26.22	10	17.54	19.46	--	line	1
								11.95	14.15	17.41	line	2
								3.25	4.21	6.93	line	3
								1.28	1.83	3.99	line	2
47	I6	B	capra	r	y	17.49	10	12.35	12.36	14.44	depression	
								4.19	4.6	3.87	line	1
								2.32	3.59	3.01	line	1
58	G6	0-10	ovis	r	y	37.22	8	32.05	33.78	--	line	2
								27.01	28.38	29.4	line	1
								24.41-20.49	26.89-23.04	25.22-22.21	pits	
								16.85	17.87	18.95	line	1
								10.07	12.41	12.12	line	1
								6.46	5.9	6.91	line	4
								4.12	4.13	4.51	line	4
								2.48	2.18	2.53	line	1
109	I6	0-10	capra	l	y	15.37	10	10.52	--	--	line	1
45	I6	B	capra	l	y	24.23	10	14.55	15.95	17.08	line	1
								12.12	12.63	12.63	line	2
								9.2	9.83	11.39	line	1
								5.86	6.04	8.1	line	2
								3.35	2.63	4.84	line	2
								2.11	1.57	3.23	line	1
46	I5	0-10	ovis	r	y	33.39	10	12.81-10.55	17.5713.95	16.8913.80	wide line	4
								7.96	9.31	9.14	depression	
49	G6	0-10	capra	r	y	33.69	7	6.82	3.72	5.77	depression	
								13.12	12.58	13.31	depression	
51	I6	B	capra	r	y	24.48	10	14.42	16.13	17.41	depression	
								12.85	15.19	16.33	depression	
								11.74	10.93	12.16	line	3
								5.96	6.5	8.33	line	2
								3.56	3.65	5.58	line	3
								2.64	2.55	3.61	line	3
50	H6	0-10	capra	r	y	35.96	6	16.28	16.43	15.27	line	1
								12.41-7.51	12.85-7.59	11.58-8.60	wide line	4

Lemek North East First and Second Molars

Sample code	SQ	Spit	Species	L / R	crown complete	Height	wear stage	M1/M2?	A Cusp hypo	P Cusp hypo	type	severity
13	G6	B	capra	r	y	29.19	6	m1	none	none		
95	G6	0-10	capra	r	n		2	m1	none	none		
99	G6	0-10	capra	r	n		2	m2	none	none		
121	G5	0-10	capra	r	y	15.68	8	m1	9.81	11.13	depression	
22	H6	0-10	capra	r	y	13.12	11	m1	6.61	6.15	depression	
22	H6	0-10	capra	r	y	25.04	8	m2	12.51	11.81	depression	
									5.85	6.46	depression	
110	I6	0-10	ovis	l	y	17.78	8	m1	13.76	16.82	depression	
18	H6	0-10	ovis	r	y	15.52	9	m2	4.43	5.78	line	2
									--	5.1	line	2
									--	2.04	line	2
105	I6	0-10	capra	r	y	10.21	9	m2?	7.68	8.36	depression	
									3.58	3.59	line	3
27	F5	B	capra	r	y	28.54	7	m2	7.57	9.79	line	1
									5	5.76	line	1
25	F6	0-10	ovis	r	y	27.47	8	m1	16.56	19.7	pits	
									2.63	4.39	line	2
25	F6	0-10	ovis		y	44.46	6	m2	32.7	33.76	pits	
									5.59	4.77	line	2
93	G6	0-10	capra	r	n			m1?	12.95	14.02	depression	
29	G6	0-10	capra	r	y	12.46	8	m1	none	none		
					y	23.81	8	m2	none	none		
28	I6	B	capra	r	y	13.93	14	m1	11.71	11.56	depression	
26	G6	B	capra	l	y	17.89	8	m1	8.74	11.24	line	2
									5.44	6.54	line	3
									3.11	4.42	line	2
									1.27	2.74	line	2
									--	0.95	line	1
?	?	?	capra	l	y	30.26	6	m2	21.42	22.48	line	1
									17.17	17.26	line	1
									15.43	15.5	pits	
									11.58	11.86	depression	
									9.42	8.24	pits	
									5.42	6.54	line	1
24	F6	B	capra	r	y	15.11	8	m2	none	none		
17	I6	B	capra	r	y	16.02	9	m2	--	13.31	depression	
									--	7.86	depression	
33	I6	B	capra	r	y	17.08	8	m2	9.74	10.07	line	1
									7.79	7.98	line	1
									3.95	4.43	line	1
30	G6	B	capra	r	y	12.43	9	m1	none	none		
14	I6	B	capra	r	y	12.33	11	m1	11.08	--	depression	
14	I6	B	capra		y	22.42	8	m2	5.79	6.1	line	1
									1.67	3.02	line	1
									--	1.3	line	1
96	I6	B	o?	r	y	21.09	8	m1?	14.01	broken	line	2
									9.48	broken	line	3
									6.02	broken	line	3
									2.68	broken	line	2
									0.92	broken	line	2
38	I6	B	capra	r	y	21.51	8	m1?	16.68	17.67	depression	
									9.44	10.32	depression	
36	F6	0-10	capra	r	y	27.89	6	m1?	8.68	10.87	depression	
1	H6	0-10	capra	r	y	25.06	7	m1?	9.57	11.7	depression	
112	F6	B	c?	r	y	13.01	9	m2?	none	none		
107	I6	0-10	capra	r	y	22.81	8	m1	12.96	15.5	depression	
									5.04	5.99	depression	
107	I6	0-10	capra		n			m2	none	none		
34	I6	B	capra	l	n	31.82	3	m2?	21.2	19.74	line	3
40	F5	B	capra	l	y	25.17	7	m1	11.73	12.83	pits/depression	
32	I6	B	capra	r	y	18.18	8	m2	9.94	10.55	line	1
									6.04	5.76	line	2
									3.13	3.4	line	2
35	I6	B	c?	r	y	14.52	9	m2?	none	none		
114	I6	B	Ovis	r	n		6	m2	1.35	1.54	line	3
									3.13-9.53	3.68-9.55	wide line	4
									11.42	--	line	3
									14.99	15.71	line	3
									18.53	20.33	line	3
									21.23-25.96	21.14-27.47	wide line	4
									broken	30.91	line	2
									broken	32.49	line	2
58	G6	0-10	ovis	r	y	16.73	8	m1	1.26	2.8	line	1
58	G6	0-10	ovis	r	y	30.58	8	m2	16.98	18.92	line	1
									13.36	--	depression	
									9.81	11.55	depression	
									7.46-5.10	7.24-5.25	wide line	4
									3.35	3.7	line	2
									2.35	2.48	line	2

Ngmuriak First and Second Molars

Sample No.	SQ	Spit	Species	L / R	wear stage	M1/M2?	Height	crown complete	A Cusp Hypo	P Cusp Hypo	type	severity
579.0	96E/145	60-70	c?	r	3	m1		n	8.79	10.31	pits	--
									17.52	17.52	depression	--
674.0	116e/355	60-70	capra	r	8	m1	21.07	y	15.12	16.92	line	1
									8.25	9.07	line	1
									3.57	4.6	line	1
									1.88	2.57	line	1
674.0	116e/355	60-70	capra	r	4	m2	33.74	n	8.38	9.66	line	1
									21.48	22.01	line	1
605.0	76e/456	30-40	capra	l	3	m1	25.5	y	13.43	11.83	line	1
									6.31	5.65	depression	
									3.6	3.53	line	1
									2.38	2.39	line	1
612.0	119e/365	99.4-99.3	capra	r	6	M1	23.34	y	1.77	2.12		1
									7.17	6.44		1
									8.82	9.19		1
									9.93	11.18		1
612.0	119e/365	99.4-99.3	capra	r	6	M2		n	none	none		
632.0	99e/21	99.8-99.7	ovis	r	6	M1	29.95	y	none	none		
					3	M2		n	none	none		
606.0	135	155-160	ovis	r	3	M1		n	9.06	7.9	depression	
603.0	99e/203	100-99.9	ovis	r	2	M2		n	none	none		
631.0	118e/36s	99.3-99.0	capra	r	broken	M1	broken	y	7.06	7.06	line	1
632.0	118e/36s	99.3-99.1	capra	r	broken	M2		n	none	none		
607.0	96e/14s	60-70	o?	r	3	M1		n	14.66	--	large pit	
									18.99	18.99	line	1
									23.92	--	large pit	
613.0	99E/20S	99.9-99.8	Capra	r		m1		n	none	none		
609.0	96e/14s	70-80	capra	r	7	?	23.78	y	12.85	13.88	depression	
									4.49	4.94	line	1
703.0	118e/35s	99.6-99.5	ovis	r	6	m2	33.87	y	none	none		
927.0	96e/145	70-80	ovis	r	8	m1	16.28	y	13.12	--	depression	
									--	4.2	pit	
									--	1.45	line	1
927.0	96e/145	70-80	ovis	r	8	m2	27.98	y	1.86	2.56	line	2
									4.58	5.13	line	3
									17.62-27.00	20.57-27.04	huge hypo	4
622.0	35.38e	61-62	capra	r		m1		y	none	none		
					8	m2	21.79	y	--	16.08	depression	
									7.32	8.09	depression	
627.0	116e/36s	99.6-99.5	c?	r	8	m1	27.59	y	none	none		
624.0	96e/215	100.0-99.9	o?	r	9	m1	12.63	y	none	none		
624.0	96e/215	100.0-99.9	o?	r	?	m2	26.41	y	16.03	19.16	depression	
629.0	130-135e	60-65	ovis	r	8	m2	15.95	y	none	none		
628.0	117e-36s	99.6-99.5	capra	r	8	m2	15.43	y	none	none		
621.0	119e-35s	99.3-99.2	capra	r	8	m1	12.15	y	2.57	3.11	depression	
622.0	119e-35s	99.3-99.3	capra	r	8	m2	20.75	y	15.13	--	depression	
									12.49	14.27	line	1
									9.21	10.49	line	1
									4.86	6.49	line	1
									2.44	3.38	line	2
									--	1.3	line	2
626.0	118e-365	99.6-99.5	c?	l	8	m2	19.91	y	--	1.89	line	1
630.0	118e-35s	99.4-99.3	?	r	8	m2	14.78	y	none	none		
666.0	140-150e 115-125s	?	ovis	l	8	m2	21.23	y	11.55-7.46	12.63-7.54	wide line	4
									3.65	4.48	line	2
633.0	86e-45s	10.0-20.0	ovis	l	7	m1	30.39	y	none	none		
634.0	86e-45s	10.0-20.1	ovis	l	2	m2		n	27.02	26.41	pit	
634.4	118e-35s	99.3-99.0	c?	l	6	m1	23.71	y	none	none		
635.4	118e-35s	99.3-99.1	c?	l	4	m2	35.93	y	none	none		
649.0	119e-35s	99.3-99.2	c?	l	9	m1	12.04	y	9.42	--	depression	
									5.13	7.32	depression	
									2.26	2.53	depression	
649.0	119e-35s	99.3-99.2	c?	l	8	m2	21	y	14.7	16.24	depression	
									10.51		line	1
									7.95	8.85	line	2
									5.1	5.91	depression	
617.0	118e-36s	99.6-99.5	capra	l	5	m2	33.88	y	4.98	5.99	line	1
									3.02	3.64	line	1
648.0	9.90E-21	99.0-99.8	?	l	8	m2	17.12	y	4.85	5.72	line	1
									3.94	4.1	line	1
									1.83	2.52	line	1
581.0	20e-127s	20-30	capra	r	7	m1	23.81	y	15.1	16.99	line	1
									7.56	7.41	depression	
581.0	20e-127s	20-30	capra	r	1	m2		n	none	none		
635.0	99e-21s	99.8-99.7	capra	l	8	m1	17.74	y	none	none		

Sample No.	SQ	Spit	Species	L / R	wear stage	M1/M2?	Height	crown complete	A Cusp Hypo	P Cusp Hypo	type	severity
636.0	99e-21s	99.8-99.8	capra	l	6	m2	29.26	y	11.97	14.87	depression	
									7.82	7.57	line	1
									6.37	6.17	line	1
636.0	117e-35s	99.6-99.5	c?	l	10	m1	13.34	y	none	none		
637.0	117e-35s	99.6-99.6	c?	l	broken	m2	broken	y	none	none		
672.0	6.60E-54	75-80	ovis	l	8	m1	32.86	y	29.09-25.40	33.17-30.29	wide line	3
									20.48	23.74	line	2
									6.63	8.55	depression	
									1.74	3.79	line	1
637.0	1.16E-35	99.3-99.2	capra	l	8	m1	17.8	y	--	7.4	depression	1
					8	m2	26.85	y	14.69	15.81	line	1
									12.45	14.25	depression	
									9.82	--	line	1
641.0	96e-24s	80-90	?	l	8	m2	14.42	y	none	none		
761.0	96e-24s	60-70	ovis	l	2	m2		n	17.35-20.71	17-20.51	wide line	3
									24.47	23.78	line	3
									28.65	27.28	line	2
889.0	130-135e	60-65	ovis	l	2	m2		n	none	none		
763.0	117e36s	99.5-99.4	capra	l	3	?m2?	36.77	y	11.55	11.15	depression	
760.0	9.60E-234	100.0-99.9	c?	l	6	?m2?	39.07	y	31.88	32.59	line	1
									18.84	21.15	line	4
									14.6	15.83	line	3
									9.81	10.74	line	1
									5.59	5.32	depression	
762.0	96e-23s	99.9-99.8	ovis	l	7	?m2?	39.66	y	25.72	27.73	line	3
									20.29	21.92	depression	
									14.82	15.86	depression	
933.0	18e-126s	sf-floor	o?	l	8	?m1?	31.03	y	13.51	14.72	depression	
									7.03	7.65	line	1
765.0	96e-14s	60-70	capra	l	7	?m1?	31.14	y	none	none		0
766.0	118e-36s	99.6-99.5	capra	l	7	?	27.95	y	--	2.29	line	1
767.0	66e-55s	75-80	c?	l	8	?	25.24	y	16.07	18.08	pits	
									6.54	7.51	line	1
647.0	118e-35s	99.3-99.2	capra	l	8	m1	15.47	y	none	none		
644.0	120e-35s	99.5-99.4	c?	l	8	m1	19.43	y	13.26	14.29	depression	
									6.67	6.29	line	1
									3.79	2.66	line	1
645.0	119e-35s	99.3-99.2	capra	l	9	m1	11.78	y	--	2.97	line	2
									--	1.07	line	1
650.0	97e-20s	99.9-99.8	capra	l	8	m1	16.98	y	9.76	10.68	line	1
									6.11	5.49	line	1
771.0	119e-35s	99.6-99.5	capra	l	3	m1		n	none	none		
773.0	96e-4n	50-60	capra	l	8	?m1?	28.91	y	1.76	--	line	1
929.0	18e-126s	sf-floor	c?	l	8	?m1?	20.01	y	1.89	2.12	line	1
774.0	140-150e/115-125	section	ovis	l	8	?m1?	broken	y	9.15	10.07	line	1
775.0	120e-35s	99.6-99.5	capra	l	8	?	28.04	y	13.22	13.44	depression	
									9.02	9.02	line	1
778.0	56e-45s	20-30	?	l	8	?	19.74	y	11.32	9.85	pit	
781.0	96e-20s	100.0-99.9	?	l	8	?	17.19	y	5.68	5.98	line	1
									4.18	4.29	line	1
931.0	96e-45s	60-70	capra	r	4	m1	33.86	y	12.02	13.38	depression	
652.0	96e-22s	99.9-99.8	capra	r	6	m2	31.23	y	21.66	22.27	line	1
									17.62	17.22	depression	
									10	10.66	line	1
									8.19	7.86	depression	
653.0	1.17E-36	99.3-99.2	capra	r	8	m1	18.94	y	--	14.76	depression	
									9.68	10.24	depression	
									1.79	1.41	line	1
653.0	1.17E-36	99.3-99.2	capra	r	7	m1	31.93	y	22.12	--	pits	
									18.75	--	line	1
									14.12	15.57	depression	
									8.62	9.18	line	1
									6.69	7.02	line	1
645.0	117e-35s	99.4-99.3	capra	r	8	m1	20.89	y	9.36	8.55	depression	
									--	3.38	pit	
645.0	117e-35s	99.4-99.3	capra	r	6	m2	30.47	y	--	14.69	depression	
									2.06	2.3	pits	
659.0	119e-35s	99.5-99.4	c?	r	8	m2	broken	y	13.71	15.72	depression	
									7.34	8.82	line	1
657.0	119e-37s	99.4-99.3	capra	r	8	m1	14.93	y	11.6	--	line	1
									8.83	8.56	line	1
					8	m2	23.24	y	18	18.58	depression	
									11.94	12.65	line	1
									3.7	3.18	line	1
658.0	118e-36s	99.3-99.2	capra	r	8	m1	13.6	y	none	none		
658.0	118e-36s	99.3-99.2	capra	r	8	m2	22.97	y	16.82	14.63	depression	
									6.75	6.83	depression	
656.0	1.19E-33	99.3-99.2	capra	r	8	m1	19.77	y	6.34	6.01	depression	
									1.8	1.06	line	1

Sample No.	SQ	Spit	Species	L / R	wear stage	M1/M2?	Height	crown complete	A Cusp Hypo	P Cusp Hypo	type	severity
656.0	1.19E-33	99.3-99.2	capra	r	6	m2	29.72	y	16.29	17.84	depression	
									10.86	11.27	depression	
									5.7	6	line	1
									1.7	1.78	line	1
									--	0.62	line	1
662.0	1.19E-31	99.3-99.2	ovis	r	9	m1	12.74	y	none	none		
663.0	1.00E+00	99.3-99.3	ovis	r	8	m2	24.85	y	--	2.54	line	1
926.0	126e-59s	65-70	capra	r	8	m1	13.43	y	none	none		
927.0	126e-59s	65-71	capra	r	8	m2	24.5	y	17.7	21.1	depression	
									5.89	6.24	line	1
668.0	56e-45s	20-30	capra	r	8	m2	24.43	y	none	none		
660.0	130-135e-55-60	outcrop section	ovis	r	11	m1	14.3	y	7.06	8.79	depression	
									4.54	6.2	line	1
660.0	130-135e-55-60	outcrop section	ovis	r	8	m2	27.24	y	11.21	13.23	depression	
									7.58	6.92	depression	
									1.36	2.32	line	1
664.0	116e-37s	99.5-99.4	capra	r	8	m2	20.43	y	2.3	2.46	line	2
665.0	116e-35s	70-80	capra	r	11	m1	11.49	y	none	none		
666.0	116e-35s	70-81	capra	r	8	m2	21.23	y	12.52	10.49	pit	
667.0	117e37s	99.6-99.5	capra	r	10	m2	16.1	y	none	none		
669.0	119e-37s	99.4-99.3	capra	r	10	m2	12.87	y	8.99	9.26	depression	
709.0	117e-36s	99.6-99.5	capra	r	8	m2	19.82	y	10.83	11.82	line	1
672.0	119e-37s	99.5-99.4	ovis	r	6	m1	32.05	y	none	none		
673.0	118e-35s	99.4-99.3	c?	r	7	m1	24.54	y	8.06	9.71	line	1
									5.58	9.17	line	2
									4.49	5.32	line	1
									1.64	2.06	line	1
673.0	118e-35s	99.4-99.3	c?	r	7	m2		n	none	none		
651.0	96e-55s	30-40	capra	r	8	m1	21.08	y	12.84	14.11	line	1
									9.47	10.08	line	1
									7.09	8.64	line	1
									2.62	2.39	line	1
651.0	96e-55s	30-40	capra	r	4	m2	33.78	n	16.79	17.38	pits	
									19.36	21.23	line	1
675.0	96e-55s	20-30	ovis	r	8	m1	23.38	y	16.65	18.27	pits	
									11.86	12.79	line	1
									8.9	9.39	line	1
									3.68	4.81	depression	
675.0	96e-55s	20-30	ovis	r	4	m2		n	15.38	14.99	depression	
676.0	140-150e/115-125s	section	ovis	r	8	m1	27.34	y	17.66	20.38	line	1
									10.46-7.19	12.15-9.17	wide line	4
									5.12	7.1	line	3
									--	3.62	line	1
									--	2.26	line	1
676.0	140-150e/115-125s	section	ovis	r	5	m2	42.29	n	3.37-7.10	3.91-6.10	wide line	3
									8.72	8.39	pits	
									10.59	10.4	line	3
									14.65	13.97	line	2
									19.22	21.76	line	2
678.0	A 25	70cm	capra	r	8	m1	23.5	y	10.12	10.44	line	1
									3.7	4.64	line	1
									1.64	2.46	line	1
678.0	A 25	70cm	capra	r	2	m2		n	none	none		
679.0	116e-35s	45-50	capra	r	8	m1	22.9	y	8.03	8.04	depression	
									3.38	3.77	line	1
680.0	116e-36s	99.4-99.3	ovis	r	8	m1	23.08	y	12.11	14.12	depression	
									3.93	2.73	line	1
									--	1.82	line	1
803.0	140-140e/115-125s	section	ovis	r	8	m1	28.08	y	10.95	12.98	depression	
									3.45	4.07	line	1
681.0	115e-37s	99.5-99.4	ovis	r	8	m1	26.58	y	11	14.78	depression	
									5.45	7.23	depression	
683.0	99e-21s	99.8-99.7	capra	r	8	m1	18.01	y	7.49	7.55	line	1
									6.4	5.82	line	1
683.0	99e-21s	99.8-99.7	capra	r	6	m2	29.63	y	--	14.22	line	1
682.0	99e-21s	99.9-99.8	capra	r	8	m1	18.67	y	12.53	14.21	depression	
									7.76	7.24	depression	
682.0	99e-21s	99.9-99.8	capra	r	6	m2	32.07	y	15.39	16.84	depression	
									13.79	14.78	depression	
									7.03	8.6	depression	
638.0	96e-21s	100.0-99.9	capra	r	8	m1	17.28	y	none	none		
639.0	96e-21s	100.0-99.10	capra	r	8	m2	33.95	y	2.72	4.63	line	2
685.0	116e-35s	40-50	capra	r	8	m1	17.28	y	3.98	3.39	line	1
685.0	116e-35s	40-50	capra	r	7	m2	27.75	y	13.64	15.31	depression	
									5.41	4.28	line	1
688.0	120e-36s	99.6-99.5	ovis	r	8	?	27.62	y	18.02	20.78	depression	
									9.36	10.19	line	1
									--	3.02	line	1

Sample No.	SQ	Spit	Species	L / R	wear stage	M1/M2?	Height	crown complete	A Cusp Hypo	P Cusp Hypo	type	severity
688.0	120e-36s	99.6-99.5	capra	r	8	?	27.94	y	21	21.19	depression	
									13.75	13.43	line	1
690.0	119e-35s	99.3-99.2	capra	r	11	m1	10	y	none	none		
691.0	119e-35s	99.3-99.3	capra	r	8	m2	16.4	y	10.37	11.18	line	1
									6.13	6.4	depression	
									4.35	--	line	1
785.0	97e-23s	100.099.9	ovis	r	6	?	43.47	y	none	none		
787.0	116e-36s	99.6-99.5	ovis	r	5	?	41.73	y	13.02	13.75	depression	
932.0	21e-130s	ash-floor	capra	r	8	?	26.35	y	none	none		
786.0	97e-22s	99.9-99.8	ovis	r	8	?	34.19	y	18.12	17.18	depression	
									6.17	8.42	depression	
1000.0	?	?	capra	r	8	?	33.86	y	none	none		
930.0	116e-35s	99.3-99.2	capra	r	2	?		n	none	none		
693.0	120e-36s	99.4-99.3	capra	r	8	m1	24.74	y	16.14	17.59	depression	
									11.84	12.22	line	1
									6.94	8.03	line	1
									--	2.43	line	1
695.0	119e-36s	99.3-99.2	?	r	8	m1	13.8	y	7.3	9.55	depression	
									--	3.49	line	1
									--	1.86	line	1
696.0	120e-35s	99.6-99.5	?	r	9	m1	17.44	y	14.83	15.81	depression	
793.0	140-150e/115-125s	section	capra	r	2	m1		n	12.66	13.31	depression	
794.0	119e-35s	99.3-99.2	capra	r		m1		n	14.18	15.74	depression	
795.0	117e-35s	99.6-99.5	capra	r		m1		n	12.75	13.08	depression	
797.0	126e-58s A2	65-70	capra	r	8	?	19.56	y	13.52	--	pit	
									9.57	9.85	line	1
									7.36	7.12	line	1
									4.78	2.16	line	
799.0	97e-23s	100.0-99.9	ovis	r	8	?	25.41	y	11.06	13.19	line	1
									6.52	7.93		1
									4.32	5.4		1
									--	3.72	line	3
800.0	96e-22s	99.9-99.8	capra	r	8	?	19.07	y	none	none		
801.0	116e-36s	99.6-99.5	capra	r	10	?	16.72	y	8.5	9.48	depression	
									4.86	6.09	line	1
									3.12	3.33	line	1
802.0	96e-21s	99.9-99.8	o?	r	8	?	14.74	y	6.06	7.33	line	1
									4.42	5.58	line	1
									2.81	2.82	line	1
804.0	117e-38s	99.4-99.3	c?	r	10	?	11.96	y	none	none		
618.0	96e-14s	65-70	o?	1	10	m1	17.35	y	10.27	10.74	depression	
619.0	126e-605sA5	60-70	C?	L	10	M1	16.81	Y	3.43	5	line	1
623.0	116E-37S	99.4-99.3	c?	1	9	m1	13.51	y	none	none		
655.0	116e-36s	99.4-99.3	capra	1	8	m1	20.86	y	none	none		
661.0	118e-36s	99.3-99.2	c?	1	8	m1	12.94	y	11.32	12.07	depression	
									4.71	4.06	line	1
11153.0	117e-50s	3rd spit	ovis	1	8	m1	20.27	y	none	none		
11154.0	117e-50s	4th spit	ovis	1	7	m2	36.54	y	21.5	24.37	pits	
									13.97	16.41	line	1
									11.96	13.41	line	1
									8.63	9.93	line	1
									4.3	4.75	line	1
11084.0	115e-49s	5th spit	ovis	1	8	?	25.79	y	13.48	13.47	depression	
11053.0	114e-48s	7th spit	ovis	1	8	m1	27.97	y	13.29	16.11	line	1
									10.14	15.08	line	2
									4.68	8.2	depression	
11053.0	114e-48s	7th spit	ovis			m2		n	none	none		

Ngmuriak Third Molars

Sample No.	SQ	Spit	Species	L / R	crown complete	Height	wear stage	A Cusp Hypo	M Cusp Hypo	P Cusp Hypo	type	severity
927.0	96e/145	70-80	ovis	r	y	39.69	8	2.15	2.09	2.59	line	2
								4.09	5.6	7.26	line	2
								13.13	15.64	18.88	line	3
								14.72	16.61	--	pit	
								16.24	19.1	22.6	line	3
								18.3-31.74	20.54-35.88	24.66-38.09	pits	
622.0	35.38e	61-62	capra	r	y	32.02	7	REJ-2.30	REJ-4.30	REJ-4.30	Wide line	4
								3.59	6.78	7.87	line	2
								10.03	13.83	14.26	depression	
								13.98	17.51	18.39	line	1
624.0	96e/215	100.0-99.9	o?	r	y	35.14	?	--	21.89	18.96	depression/pits	
								14.63	15.84	13.41	line	1
								--	7.85	5	line	2
									4.61	4.2	line	1
									2.84	3.18	line	2
									1.92	--	line	1
629.0	130-135e	60-65	ovis	r	y	25.38	10	20.54-15.75	21.95-19.14	24.95-22.39	wide line	4
								14.52	16.31	18.82	line	3
								11.75	12.72	15.78	line	4
								9.58	9.72	11.61	line	2
								6.13	7.14	8.54	line	2
								3.04	2.98	4.86	line	4
628.0	117e-36s	99.6-99.5	capra	r	y	26.46	8	9.57	8.49	10.34	depression	
621.0	119e-35s	99.3-99.2	capra	r	y	29.25	8	10.23	11.34	13.64	line	2
								8.18	9.76	11.76	line	2
626.0	118e-365	99.6-99.5	c?	l	y	30.43	9	22.52	22.97	22.69	depression	
								8.63	10.15	9.56	line	1
								4.59	5.25	6.19	line	1
										3.76	pit	
716.0	9.7E-204	100.0-99.9	ovis	r	y	broken	4	25.92	28.24	27.62	line	2
								22.25-15.88	22.16-16.35	22.02-17.80	Wide line	3
								13.4	14.67	14.35	line	2
								10.19	10.54	11.33	line	4
								8.14	8.86	9.52	line	2
								4.14	4.29	4.77	line	4
714.0	96-e-45	50-60	?	r	n		2	none	none	none		
715.0	9.9E-20	99.9-99.8	ovis	r	n		2	none	none	none		
717.0	9.6E-144	60-70	ovis	r	n		3	none	none	none		
719.0	117e-555	99.3-99.2	capra	r	y	18.89	16	17.01	--	--	line	1
								14.16	14.27	15.69	line	1
								11.5	11.64	--	line	1
								8.5	8.87	10.1	line	1
								5.16	5.05	4.23	line	1
720.0	1.18E-33	99.3-99.2	c?	r	y	29.15	8	15.46	--	--	line	1
								8.32	10	13.67	line	1
								4.32	5.93	--	line	1
								--	--	3.58	line	2
630.0	118e-35s	99.4-99.3	?	r	y	22.58	10	9.63	11.12	12.12	depression	
								5.15	5.28	7.83	line	1
								--	2.42	4.66	line	1
										1.5	line	1
724.0	118e-36s	99.6-99.5	c?	r	y	30.83	9	17.3	18.64	17.5	line	1
								10.17	10.68	11.07	line	1
								8.61	9.07	9.09	line	1
666.0	0-150e 115-1	?	ovis	l	y	26.83	10	13.13	16.6	19.17	line	3
								11.69-9.91	13.91-11.84	17.64-15.13	Wide line	4
								7.79	10.45	12.9	2	3
								5.96	9.58	11.22	2	2
								4.59-REJ	6.43-4.10	9.19-REJ	Wide line	3
722.0	96E-24S	1	c?	l	y	25.81	10	none	none	none		
721.1	119e-37s	99.6-99.5	capra	l	y	31.25	8	6.56	7.64	9.62	line	1
								3.74	3.44	4.9	line	2
									1.15	2.86	line	2
										1.39	line	2
727.0	117e-36s	99.6-99.5	o?	l	y	14.53	10	none	none	none		
728.0	130-135e	60-65 s	c?	l	y	18.84	10	9.03	11.19	--	line	1
								6.25	5.77	6.89	depression	
								4.43	--	4.1	line	1
								--	2.74	2.63	line	2
729.0	118e-37s	99.3-99.0	1	l	y	15.14	10	9.79	7.27	8.24	depression	
								--	2.54	3.39	line	1
652.0	96e-22s	99.9-99.8	capra	r	n		2	none	none	none		
659.0	119e-35s	99.5-99.4	c?	r	n		2	27.5	25.29	21.15	depression	
657.0	119e-37s	99.4-99.3	capra	r	y	31.57	8	17.75	19.8	20.9	Line	1
								11.56	13.57	14.29	depression	
658.0	118e-36s	99.3-99.2	capra	r	y	30.25	8	--	15.17	--	pit	
								9.23	10.3	11.32	depression	

Sample No.	SQ	Spit	Species	L / R	crown complete	Height	wear stage	A Cusp Hypo	M Cusp Hypo	P Cusp Hypo	type	severity
656.0	1.19E-33	99.3-99.2	capra	r	n		2	19.44	18.96	--	depression	
662.0	1.19E-31	99.3-99.2	ovis	r	y	32.95	9	--	3.88	6.41	line	2
668.0	56e-45s	20-30	capra	r	n		4	24	26.12	--	depression	
660.0	80-135e-55-6	outcrop section	ovis	r	y	35.7	8	18.14	19.07	19.99	line	2
								11.6	12.98	15.62	pits	
664.0	116e-37s	99.5-99.4	capra	r	y	29.68	10	6.25	7.03	7.71	line	2
								4.69	4.08	5.43	line	2
								3.41	1.45	3.43	line	2
665.0	116e-35s	70-80	capra	r	y	28.82	8	20.04	20.74	--	line	1
								12.52	15.05	16.03	line	2
								10.47	12.23	--	line	2
								6.28	6.78	7.47	line	1
								2.99	--	--	line	1
667.0	117e37s	99.6-99.5	capra	r	y	25.22	9	7.38	7.24	9.83	depression	
669.0	119e-37s	99.4-99.3	capra	r	y	19.11	10	6.45	7.14	8.21	line	1
								3.08	3.22	4.38	line	2
								1.61	2.23	2.25	line	1
699.0	99e-21s	99.9-99.8	capra	r	n			none	none			
704.0	116e-35s	99.6-99.5	capra	r	y	33.82	3	none	none	none		
702.0	99e-22s	99.9-99.8	ovis	r	y	44.75	4	none	none	none		
705.0	118e-36s	99.6-99.5	ovis	r	y	41.09	5	none	none	none		
706.0	117e-37s	99.5-99.4	ovis	r	y	40.26	8	10.24	--	--	line	1
709.0	117e-36s	99.6-99.5	capra	r	y	30.14	9	16.36	17.36	16.7	line	1
								14.15	15.3	--	line	1
								1.29	2.41	2.88	line	1
								--	1.48	1.54	line	1
687.0	118e-37s	99.6-99.5	capra	r	y	31.14	4	23.05	24.82	23.67	depression	
11153.0	117e-50s	3rd spit	ovis	l	y	46.21	4	none	none	none		

Narosura First and Second Molars

sample no.	SQ	Spit	Species	L / R	Height	wear stage	M1/M2?	crown comp	A Cusp hypo	P Cusp hypo	type	severity
8.8	E16	70-80	Capra	r	13.09	8	m1	y	none	none		
45.5	C11-D9	60-70	ovis	r	21.03	8	m1	y	10.2	10.56	depression	
									2.04	3.43	line	2
14	D16	70-80	capra	r	19.47	8	m1	y	11.16	10.71	depression	
									3.41	2.87	line	1
21.1	D16	80-90	capra	L	14.93	8	M1	y	10.14	12.07	pits	
									6.79	6.01	depression	
21.1	D16	80-90	capra	L	26.63	8	m2	y	9.98	10.17	line	3
									9.41	7.67	pits	
									1.84	2.19	line	2
11.8	?	?	capra	r	32.45	7	m2	y	12.57	12.57	line	1
									10.17	10.17	line	1
									4.33	4.33	line	1
11.8	?	?	capra	r	18.29	8	m1	y	14.79	15.89	line	1
									2.75	3.12	line	1
									1.8	1.28	line	1
?	F14	70-80	capra	1	25.53	8	m1	y	12.99	15.32	depression	
?	E14	80-90	Capra	r	12.3	8	m1	y	7.21	8.19	depression	
?	E14	80-90	Capra	r	18.94	8	m2	y	none	none		
?	E15	80-91	Capra	r	22.09	8	m2	y	none	none		
4.5	f14	70-80	Capra	r	25.07	8	m1?	y	none	none		
5.8	E12	80-90	ovis	r	broken	8	m1?	y	27.64	--	line	1
									22.56	25.58	line	1
									17.1	18.88	line	1
									13.74	15.02	depression	
									6.5	7.72	depression	
5.6	e12	80-90	ovis	r	28.71	8	m1?	y	12.82	14.05	depression	
									2.36	2.08	line	1
2.8	d17	90-100	capra	r	13.14	11	m1?	y	--	10.1	pit	
3.9	d16	60-70	ovis	r	25.99	8	m1?	y	18.53-15.67	19.96-14.91	pits	
									12.98	12.23	line	2
									8.84	7.96	line	2
									7.37	6.96	line	2
3	e16	80-90	capra	r	22.07	8	m1?	y	10.35	12.15	depression	
3.4	e14	70-80	capra	r	20.72	8	m1?	y	9.41	12.24	depression	
3.1	e14	70-80	ovis	r	18.29	8	m1?	y	11.98	12.44	line	2
2.8	e12	80-90	ovis	r	20.48	8	m1?	y	none	none		
2.5	d16	60-70	capra	r	19.92	8	m1?	y	11.43	12.56	depression	
3.1	d16	60-70	ovis	r	24.66	8	m1?	y	15.83	18.93	pits	
3.1	f12	70-80	ovis	r	21.04	8	m1?	y	16.07	18.69	depression	
5.9	d16	70-80	Capra	r	32.42	8	m1?	y	26.61	25.28	line	1
									14.36	14.67	line	1
									13.09	13.1	line	1
									7.25	7.02	depression	
6.9	d12	70-80	ovis	r	26.39	8	m1?	y	13.55	17.14	pits	
									11.45	14.6	line	1
									9.81	11.74	line	1
2.9	e16	60-70	capra	r	17.16	8	m1?	y	3.78	2.86	depression	
3.8	c11-d9	60-70	ovis	1	22.92	8	,m1?	y	13.82	18.42	line	2
									12.17	14.71	line	1
									9.41	12.25	line	2
									6.94	9.58	line	4
									4.37	6.33	line	4
									3.97	4.53	line	3
									--	4.15	line	3
?	d17	70-80	ovis	1	22.08	8	m1?	y	none	none		
3.1		70-80	Capra	1	21.02	8	m1?	y	none	none		
4.8	d12	70-80	Capra	1	28.13	8	m1?	y	11.41	14.04	depression	
									7.97	8.8	depression	
4.09	d17	80-90	capra	r	25.47	8	m1?	y	none	none		
4.19	f14	80-90	capra	r	27.92	8	m1?	y	none	none		
3.9	d14	70-80	Capra	r	27.34	7	m1?	y	7.35	6.22	line	1
3.09	e16	50-60	Capra	r	22.93	8	m1?	y	11	--	depression	
3.5	f12	80-90	Capra	r	24.23	8	m1?	y	none	none		0
4.5	d16	70-80	ovis	1	24.6	8	m1?	y	14.72	18.36	depression	
									7.18	8.28	depression	
										1.61	line	1
9.7	d14	70-80	capra	r	31.3	7	m1?	y	--	13.07	pit	
2.8	d14	80-90	Capra	1			m1?	n	16.2	13.63	line	2
1.8	f12	60-70	Capra	1			m1?	n	none	none		
4.7	d14	90-100	ovis	1			m1?	n	none	none		

sample no.	SQ	Spit	Species	L / R	Height	wear stage	M1/M2?	crown comp	A Cusp hypo	P Cusp hypo	type	severity
7	i16	70-80	ovis	r	25.3	8	m1?	y	14.01	19.68	line	2
									10.07	--	pit	
									--	4	line	2
3.4	c11-d9	50-60	capra	r	22.29	8	m1?	y	none	none		
2.9	e12-e14	section	Capra	r	20.3	8	m1?	y	12.95	14.17	depression	
									10.51	12.02	pits	
3.9	110-90-10	90-100	ovis	r	24.88	8	m1?	y	none	none		
3.2	d14	70-80	Capra	r			m1?	n	none	none		
2	?	?	Capra	r				n	none	none		
2.8	e16	80-90	Capra	r	19.84	8	m1?	y	9.74	11.5	line	3
2.2	e12-f12	68-80	Capra	r	19.29	8	m1?	y	none	none		
2.4	e12-f12	68-80	Capra	r	10.83	14	m1?	y	7.98	7.96	depression	
2.7	f12	50-60	Capra	r	16	8	m1?	y	13	12.75		
4.4	d14	60-70	Capra	r	27.53	8	m1?	y	none	none		
3.2	d17	80-90	Capra	r	21.13	8	m1?	y	3.96	6.19	line	2
4.5	e17	80-90	ovis	r	24.1	8	m2?	y	none	none		
4.3	d14	70-80	ovis	r	33.88	8	m1?	y	13.62	16.39	depression	
									3.47	4.56	line	1
3.6	f14	80-80	ovis	l	23.59	8	m1?	y	none	none		
3.8	d17	80-90	Capra	r	22.91	8	m1?	y	13.28	15.11	depression	
									10.16	12.04	pits	
									6.79	7.12	depression	
4.3	d16	70-80	ovis	r	24.49	8	m1?	y	11.65	12.64	depression	
5.8	d14	70-80	capra	r	23.88	8	m1?	y	13.2	15.36	depression	
7.5	?	?	Ovis	r	41.81	6	m2?	y	36.9-32.65	39.44-36.44	wide line	4
									29.14-24.10	32.12-27.40	wide line	4
									21.4615.42	24.75-16.97	wide line	4
									13.06	16.46	line	4
									11.92	14.41	line	4
									7.65	7.78	line	4
									4.89	5.74	line	4
									--	2.48	line	2
7.7	d17	90-100	ovis	r	42.29	6	m2?	y	10.05	10.79	line	1
8.4	e14	80-90	Ovis	l	broken	8	m2?	y	32.16	33.16	depression	
6	e14	80-90	Ovis	r	36.27	8	m2?	y	none	none		
5.2	d17	90-100	capra	r	33.3	6	m2?	y	25.2	--	line	2
									4.72	--	line	2
5.4	test pit 14	--	capra	l	broken	8	m2?	y	14.23	18.21	line	3
									14.31	15.75	line	3
									12.06	14.44	line	2
									1.56	2.94	line	2
3.3	f12	70-80	capra	l	31.02	8	m2?	y	10.66	13.18	pit	
									7.47	9.34	depression	
8	e16	50-60	ovis	l	40.54	6	m2?	y	34.34-31.91	37.01-34.16	wide line	3
									28.14	32.01	line	2
									24.36	26.95	line	2
									21.58	22.83	line	2
5.2	e14	80-90	ovis	r	34.98	8	m2?	y	27.9	32.04	line	1
									13.78	16.9	line	3
									10	8.92	line	2
									6.8	4.96	line	2
5.5	f12	70-80	capra	l	33.99	8	m2?	y	none	none		
7.8	d16	70-80	ovis	l	41.19	6	m2?	y	39.06-26.80	39.34-30.19	wide line	3
									24.11	25.21	line	2
									22.3	21.76	line	2
									1.91	1.69	line	2
5	d17	90-?	capra	l	33.74	8	m2?	y	8.57	12.17	line	1
5.8	d17	80-90	capra	l	34.1	8	m2?	y	none	none		
4.1	f12	70-80	capra	l	23.24	8	m2?	y	14.06	17.7	depression	
									9.3	10.95	depression	
									4.52	5.43	depression	
4.3	e14	80-90	ovis	l				n	none	none		
5.2	f12	80-90	capra	r	30.5	8	m2?	y	13.66	16.39	depression	
									3.64	4.15	line	2
									--	1.52	line	2
7.7	70-80	70-80	ovis	l	42.54	6	m2?	y	33.06	--	line	1
									29.37	--	line	1
									22.79	25.32	line	1

Narosura Third Molars

sample no.	SQ	Spit	Species	L / R	Crown complete?	Hight	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
45.5	C11-D9	60-70	ovis	r	y	47.22	8	33.44	35.24	33.36	line	2
								26.17-21.91	27.35-23.62	24.39-20.48	pits	
								19.71-17.70	21.52-19.50	17.87-15.97	wide line	4
								16.21-13.97	17.83-14.36	13.68-10.71	wide line	4
?	F14	60-70	Ovis	r	y	41.09	8	27.37-22.96	30.66-27.72	30.76-27.43	wide line	4
								19.95	24.35	25.52	line	3
								17.36	22.12	22.45	line	3
								5.99	9.52	9.21	depression	
6.3	e12	80-90	ovis	r	y	31.59	7	7.21	8.54	12.41	depression	
8.1	?	?	ovis	l	y	38.03	10	33.01-29.83	35.42-32.67	--	wide line	4
								26.9-21.37	26.53-23.81	23.22-20.65	wide line	4
								16.45	19.13	20.3	line	4
								12.49-10.69	15.64-12.53	14.89-12.65	wide line	4
								8.43	9.76	9.77	line	4
								2.65	3.65	4.81	line	4
8.6	f14	80-90	ovis	r	y	37.34	10	13.84	16.29	15.99	line	4
								12.38	13.48	15.27	line	4
								3.17	2.86	3.9	depression	
5.6	test pit 1	--	capra	r	y	30.58	7	none	none			
5.4	?	?	ovis	r	y	26.87	10	12.89-11.38	16.36-14.52	20.8-19.12	wide line	4
								8.67	11.47	15.61	line	3
								2.78	5.7	9.17	line	3
										4.51	line	3
8.6	d17	80-90	capra	r	y	35.07	8	9.4	10.09	11.89	depression	
								1.7	2.75	4.68	line	2
9.3	d14	70-80	ovis	r	n			none	none			
8.6	d14	70-80	ovis	r	y	37.39	10	29.39	32.71	--	line	1
								18.35	24.01	--	line	1
								14.24	18.55	--	line	1
								6.78	8.5	--	line	1
								1.82	2.32	--	line	1
8.3	f14	50-60	ovis		y	36.78	10	14.89	16.54	14.68	line	2
								9.02	9.86	8.71	line	3
								3.24	3.53	--	line	3
6.9	c11-d9	60-70	ovis		n		1	10.51-14.47	5.83-9.19	--	wide line	4
								19.19	13.75	--	line	3
								21.86-24.32	16.98-19.52	--	wide line	4
								28.54	23.15	--	line	3
								31.93	28.46	--	line	3
5.1	e16	80-90	ovis	r	y	19.19	10	18.25	22.69	--	line	4
								11.78	14.22	16.3	line	2
								8.67	9.82	10.94	line	3
								3.98	6.75	7.69	line	4
								--	--	4.8	line	3
								--	--	3.02	line	3
6.9	d16	80-90	ovis	r	y	19.65	10	none	none			
7.1	e16	70-80	ovis	r	y	23.83	10	12.21	10.75	--	line	4
5.7	d14	70-80	capra		n			none	none			
10	test pit 1	--	ovis	r	n			none	none			
6.6	e16	80-90	capra	r	y	36.2	9	11.84	12.57	13.78	depression	
								6.87	8.34	--	line	1
								2.2	3.77	--	line	1
6	e12	90-100	capra	r	y	32.83	10	5.29	3.98	3.14	line	3
7.8	f12	60-70	ovis	r	y	29.33	10	none	none	n		
8	f12	80-90	capra	l	y	33.77	10	12.97	15.07	--	pit/line	1
								8.9	9.72	9.98	line	1
									3.71	3.79	line	1
8	d12	60-70	capra	r	y	22.33	10	8.87	14.91	15.94	line	2
								8.01	9.78	10.35	line	3
								3.03	5.89	6.17	line	4
									3.4	3.93	line	3
										2.08	line	2
6.9	f14	70-80	capra	l	y	25.38	10	11.29	13.57	14.93	line	3
								8.8	9.49	11.74	line	3
								8.14	9.45	7.83	line	2
								5.28	5.97	3.78	line	2
14.1	e16	80-90	ovis	l	y	33.85	10	27.47	31.77	31.6	line	2
								20.07-15.95	22.41-19.22	22.31-18.26	wide line	3
								13.21	15.96	16.61	depression	
								5.59	6.98	--	line	2
								1.68	2.36	--	line	2
9.9	e12	80-90	ovis	l	y	43.81	5	20.15	22.57	22.63	line	3
								9.87	11.81	12.7	line	3
								7.72	8.96	9.61	line	3
								5.58	6.9	7.47	line	3
9.3	e16	70-80	capra	l	y	37.37	4	11.11	12.08	12.91	depression	
9.2	d17	80-90	capra	l	y	34.64	10	11.52	11.98	11.51	line	2
								6.35	7.29	--	line	3
7.2	f12	60-70	ovis	l	n		3	none	none	none		
4.9	test pit 13	--	capra	l	y	22.32	10	none	none	none		
5.9	d14	60-70	capra	r	y	broken	3	30.11	--	--	depression	

Enkapune Ya Muto First and Second Molars

Sample No.	SQ	Spit	Species	L / R	Height	wear stage	M1/M2?	crown complete?	A Cusp Hypo	P Cusp Hypo	type	severity
5137	e11/n10	105-115	capra	r	26.49	8	m1?	y	22.26	25.64	pits	
									17.24	20.29	depression	
									11.08	12.54	line	1
									9.59	10.29	line	1
4778	e11/n10	85-95	ovis	r	37.23	8	m2?	y	21.64	23.22	line	1
									8.8	8.97	line	1
									4.56	4.4	line	1
									1.64	1.55	line	2
5171	e11/n10	125-135	capra	l	broken	5	m2?	y	13.61-9.22	13.19-9.41	wide line	4
4805	e9/n10	95-105	capra	l	28.88	8	m1?	y	19.98-17.40	23.52-21.41	pits	4
									13.36	15.69	line	2
									2.14	3.08	line	2
										1.77	line	3
5042	e10-n10	?	capra	r	24.11	8	m1?	y	20.01-17.44	--	wide line	4
									14.06	--	line	3
									10.98-7.10	--	wide line	4
									5.36	--	line	2
									3.26	--	line	2
4361	e8/n10	120-140	capra	r	34.67	8	m2?	y	26.39	27.6	depression	
									16.65	16.68	depression	
									2.28	1.58	line	1
5134	e11/n10	102-115	ovis	l	32.17	8	m2?	y	17.45	21.15	pits	
									--	7.49	line	1
									--	6.18	line	2
									--	4.09	line	2
5026	e10/n10	125-140	capra	l	34.72	8	m2?	y	18.11-16.65	22.32-18.56	wide line	4
									13.06	15.06	depression	
									5.56	6.62	line	4
									4.68	4.97	line	3
									1.38	2.14	line	2
5024	e10	125-140	capra	r	19.53	8	m1?	y	5.28	4.81	line	1
5215	surface	12 nest	ovis	r	22.75	8	m1	y	none	none		
5215	surface	13 nest	ovis			4	m2	n	none	none		
4268	e8/n10	75-80	ovis	l	26.63	8	m1	y	12.87-10.19	--	lines	3
									6.96	--	lines	3
									4.76	5.59	lines	2
									3.95	--	lines	2
4268	e8/n10	75-80	ovis		38.81	4	m2	y	33.6	36.32	pits	
									28.15-24.63	30.9-28.36	wide line	4
									21.22	24.01	lines	3
									17.94-16.35	20.52-18.71	pits	
									8.99	10.92	depression	
									6.22	7.15	lines	3
									1.57	3.33	lines	2
5191	e11/n10	125-135	caprine	r	27.86	7	m2?	y	15.46-12.50	13.21-10.75	wide line	3
									8.77	9.78	line	3
									5.72	7.28	line	3
5178	e11/n10	125-135	caprine	r		2	m2?	n	1.84-6.20	1.22-2.32	pits	2
									8.67	6.14	line	2
									13.94	11.09	line	2
									20.04	17.61	line	2
5203	e11/n10	135-145	caprine	r	33.4	8	m2?	y	19.67	24.21	line	2
									8.46	10.68	line	2
									5.63	7.37	line	2
384 (0/c 5)	e7/n10	85-90	capra	l	29.87	8	m2?	y	10.88	13.5	line	2
									5.28	7.74	line	2
5136	e11/n10	105-115	ovis	r	38.68	6	m2?	y	12.09	15.56	line	1
									11.14	12.5	line	1
5475-5479	surface	--	capra	r		6	m2?	n	--	21.83	pits	
4983	e10/n10	95-105	ovis	r		5	m2?	n	26.37	27.28	line	2
4978	e10/n10	95-105	ovis	r	29.19	8	m1?	y	6.86	7.87	line	2
5025	e10/n10	125-140	capra	r	20.5	8	m1?	y	14.47	18.33	line	2
									11.7	13.61	line	1
									7.96	10.31	line	1
									--	2.64	line	2

Enkapune Ya Muto Third Molars

No	SQ	Spit	Species	L / R	Crown complete?	Height	width	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
5129	e11/n10	105-115	capra	r	y	--		4	39.03	37.97	--	line	3
									36.69	--	--	line	3
									34.1	32.02	--	line	3
5184	e11/n10	125-135	capra	l	y	34.3	7.82	5	30.73	32.28	--	pits	
									26.16	28.29	--	line	2
									23.1	24.17	--	line	2
									19.41	20.05	20.61	line	2
									15.66	16.51	15.5	line	2
									8.39	8.83	9.38	line	3
									5.85	6.35	8.27	line	4
									2.41	2.95	3.74	line	2
5149	e11/n10	115-125	ovis	l	n			1	25.8-34.28	22.62-28.37	18.2-24.66	pits	
4363	e8/n10	120-140	ovis	l	y	42.21	8.66	8	27.64-23.31	--	28.45-25.81	pits	
									15.93-13.00	17.01	17.77	pits	
									3.58	4.1	4.12	line	
5034	e19/n10	?	ovis	r	y	34.01	8.58	10	32.59	isotope analysis	31.29	pits	
									29.86-24.86	isotope analysis	--	wide line	4
									21.13	isotope analysis	--	line	2
									14.05	isotope analysis	--	line	2
									11.72	isotope analysis	--	line	2
									8.43	isotope analysis	--	line	1
									5.04	isotope analysis	--	line	1
5023 (EYM 0/c 2 m3)	e10/n10	125-140	caprine	l	n			4	isotopic analysis	10.11-15.76	7.66-11.54	pits	
1660	e11-e12	50-60	ovis	l	n			4	7.19	5.02	--	line	3
									12.32	10.85	--	line	3
									16.37	15.24	--	line	3
									22.46	21.15	--	line	4
									25.41	23.97	--	line	3

Appendix 4: Raw data from Iceland

NB: 'Height' refers to the height of the tooth crown and where a tooth crown is recorded as incomplete the location of enamel hypoplasia is recorded from the occlusal tip of the tooth following the methodology discussed in Chapter 4.

Svalbarð First Molars

Sample No.	Date	age group	L / R	Crown complete?	Height	vear stag	A Cusp hypo	P Cusp hypo	type	severity
4	pre 1300	c	l	y	28.69	2	none	none		
6	pre 1300	f	r	y	8.98	11	none	none		
7	post 1477	e	l	y	26.95	6	15.33	18.61	pit	
							9.99	13.09	pit	
							none	2.14	line	2
8	post 1477	f/g	l	y	12.31	8	none	none		
9	post 1477	e	l	y	17.58	8	none	none		
11	pre 1300	c	l	y	23.7	4	19.89	20.84	depression	
12	pre 1300	c	r	n	29.8	2	none	none		
13	pre 1300	c	r	n	28.3	3	none	16.01	pits	
14	pre 1300	c	l	y	28.31	5	none	20.37	line	1
22	post 1477	d	r	y	25.58	8	18.89	21.67	depression	
							9.9	12.52	depression	
23	post 1477	d	r	y	22.65	7	13.46	17.68	depression	
26	post 1477	f	l	y	17.44	8	none	none		
27	post 1477	d	l	y	23.56	8	none	none		
36	pre 1300	c		n	30.87	3	none	none		
37	pre 1300	c	r	y	29.21	4	20.07	20.56	line	1
							14.81	14.25	depression	
42	post 1477	f	r	y	15	8	9.77	14.98	line	1
44	pre 1300	e	l	y	14.76	8	none	none		
45	pre 1300	c	r	n	29.4	2	none	none		
46	pre 1300	c	l	n	27.11	2	none	none		
47	pre 1300	c	r	y	28.07	2	17.95	19.37	line	1
49	pre 1300	c	r	y	28.37	2	none	none		
54	pre 1300	c	l	y	30.17	2	21.1	24.24	line	1
55	pre 1300	c	l	y	27.13	2	20.27	21.29	line	1
60	pre 1300	e	r	y	16.82	8	3.08	4.07	line	4
61	pre 1300	d	r	y	20.24	8	15.36	16.83	depression	
69	pre 1300	F	r	y	12.11	8	none	none	--	--
71	pre 1300	e	l	y	15.75	8	none	none		
72	pre 1300	e	r	y	14.72	8	none	none		
73	pre 1300	d	r	y	18.58	8	none	none		
81	post 1477	f	r	y	10.98	11	none	none		
83	post 1477	d	l	y	24.22	8	14.32	17.94	line	1
							7.37	8.95	depression	
							1.69	3.8	line	1
87	pre 1300	d	l	y	18.48	8	none	none		
88	pre 1300	d	l	y	18.46	8	6	5.22	depression	
89	pre 1300	d	r	y	21.74	8	none	none		

Sample No.	Date	age group	L / R	Crown complete?	Height	vear stag	A Cusp hypo	P Cusp hypo	type	severity
94	pre 1300	c	r	n	28.46	2	none	none		
95	pre 1300	c	l	n	27.4	3	none	none		
100	pre 1300	d	r	y	19.21	8	none	none		
106	post 1477	d	l	y	24.46	8	none	none		
107	post 1477	c	r	y	31	3	24.97	23.86	line	1
109	post 1477	d	r	y	24.77	7	none	none		
110	post 1477	d	r	y	20.75	8	none	none		
114	post 1477	c	r	y	26.75	3	none	none		
116	post 1477	c	l	n	30.57	2	none	none		
120	pre 1300	e	r	y	15.87	8	9.83	11.88	depression	
							1.3	2.71	line	4
122	post 1477	d	r	y	27.3	7	24.01	22.91	depression	
							11.54	9.96	depression	
123	post 1477	f	r	y	22	8	none	none		
128	post 1477	f	l	y	7.89	11	5.34	8.68	line	1
							none	5.36	line	1
							none	none		
128	post 1477	c	l	y	22.59	7	none	15.91	pits	
							none	10.53	pits	
134	pre 1300	e	l	y	16.42	8	3.97	3.97	depression	
137	pre 1300	f	r	y	14.14	11	none	none		
138	pre 1300	F	r	y	14.53	9	11.79	14.79	line	1
							6.15	6.8	depression	
141	post 1477	e	3	y	16.29	8	none	none		
143	post 1477	e	r	y	15.06	8	5.68	7.38	depression	
144	post 1477	c	l	y	30.28	2	none	none		
145	post 1477	d	l	y	24.32	7	17.97	20.63	depression	
							14.52	14.09	depression	
							2.92	3.4	depression	
147	post 1477	d	l	y	19.62	8	11.15	14.16	depression	
148	post 1477	c	r	y	23.99	7	17.34	20.63	line	1
149	post 1477	f	l	y	14.85	8	none	none		
153	pre 1300	c	r	y	29.27	5	none	none		
154	post 1477	f	r	y	16.55	8	10.72	9.13	depression	
155	pre 1300	f	l	y	8.94	13	3.19	2.36	line	1
156	pre 1300	e	l	y	13.77	8	none	11.76	pits	
160	pre 1300	d	r	y	21.34	8	6.4	8.2	line	1
							none	4.81	pits	
163	pre 1300	c	r	y	30.23	3	none	none		
165	post 1477	f	r	y	16.14	8	none	none		
166	pre 1300	c	r	y	24.78	8	8.52	7.4	line	1
167	pre 1300	e	l	y	18.48	8	3.19	3.7	line	1
168	pre 1300	e	l	y	15.24	8	none	none		
169	pre 1300	c	r	n	29.79	2	6.84	6.33	line	1
172	pre 1300	f	r	y	16.76	8	12	14.43	line	1
							none	3.26	line	1
173	pre 1300	f	r	y	8.97	11	none	none		

Svalbarð Second Molars

Sample No.	Date	age group	L / R	Crown complete?	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
6	pre 1300	f	r	y	22.51	8	none	none		
7	post 1477	e	l	n	39.27	3	none	none		
8	post 1477	f/g	l	y	24.86	8	5.33	6.34	depression	
9	post 1477	e	l	y	30.53	8	15.17	19.62	line	1
							10.95	12.99	line	2
							6.13	8.59	line	2
							2.74	2.44	line	2
22	post 1477	d	r	y	42.52	5	19.74	20.93	depression	
							14.41	none	pits	
23	post 1477	d	r	n	32.2	2	none	none		
26	post 1477	f	l	y	30.55	8	14.74	17.15	line	2
							9.72	11.44	line	2
							6.77	9.04	line	2
								2.9	line	3
41	pre 1300	f	r	y	32.05	7	none	none		
42	post 1477	f	r	y	26.99	8	13.1	14.28	line	2
							10.45	11.92	line	2
								9.67	pit	
44	pre 1300	e	l	y	29.07	7	none	none		
60	pre 1300	e	r	y	30.84	7	22.32	25.3	pits	
							18.54	22.04	line	3
							15.73	17.89	line	2
							8.22	9.28	line	1
61	pre 1300	d	r	y	37.04	9	11.72	12.63	depression	
62	pre 1300	d	l	y	32.23	8	6.6	7.16	line	1
69	pre 1300	F	r	y	24.97	8	2.7	3.51	line	2
							none	1.04	pit	
71	pre 1300	e	l	y	30.32	7	13.32	15.89	line	1
							12.74	14.13	line	1
							10.19	12.25	line	1
72	pre 1300	e	r	y	30.32	8	12.57	15.13	line	2
							9.07	11.41	line	2
							6.49	7.81	line	2
							3.35	3.85	line	2
73	pre 1300	d	r	y	34.4	3	none	none		
81	post 1477	f	r	y	23.51	8	none	6.63	depression	
83	post 1477	d	l	y	37.65	6	10.11	10.48	depression	
							6.64	7.13	depression	
87	pre 1300	d	l	y	31.45	8	none	none		
88	pre 1300	d	l	y	30.55	8	7.96	9.29	depression	
							none	18.37	depression	
97	pre 1300	e	l	y	31.02	7	2.51	3.81	line	2
100	pre 1300	d	r	n	33.23	2	none	none		
109	post 1477	d	r	y	38.31	2	21.51	22.85	depression	
110	post 1477	d	r	y	35.86	7	none	none		
120	pre 1300	e	r	y	29.86	7	23	26.68	line	4
							19.38	23.36	line	4
							16.71	20.24	line	4
							18.7	14.73	line	4
							10.46	13.73	line	2
							6.47	7.99	line	1
							4.64	4.96	line	1
122	post 1477	d	r	n	29.01		9.02	none	pits	
							18.03	15.01	pits	
123	post 1477	f	r	y	36.66	7	13.83	16.72	depression	
							7.44	7.86	depression	
128	post 1477	f	l	y	19.53	8	13	16.63	line	1
							9.68	12.46	line	2
							none	1.98	line	1
128	post 1477	c	l	n	30.7	1	none	none		
134	pre 1300	e	l	y	30.44	8	none	none		
137	pre 1300	f	r	y	26.22	8	15.53	18.13	line	2
							7.21	6.87	depression	
138	pre 1300	F	r	y	26.67	8	17.2	19.53	depression	
							13.05	13.29	depression	
							9.65	10.22	pit/depression	

Sample No.	Date	age group	L / R	Crown complete?	Height	wear stage	A Cusp hypo	P Cusp hypo	type	severity
141	post 1477	e	3	y	31.68	8	12.58	16.8	line	1
							4.39	6.31	pit	
							4.4	1.46	line	3
							none	0.87	line	2
143	post 1477	e	r	y	30.07	8	14.47	16.3	depression	
							9.24	10.49	line	2
145	post 1477	d	1	n	32.28	2	none	none		
147	post 1477	d	1	y	34.88	6	10.45	10.93	line	2
							6.39	4.92	line	2
148	post 1477	c	r	n	32.34		none	none		
149	post 1477	f	1	y	28.21	8	16.39	19.34	line	2
							8.6	9.15	depression	
152	pre 1300	e	r	y	28.58	8	15.46	14.24	pit	
							none	9.77	pit	
153	pre 1300	c	r	n	34.03	1	none	none		
154	post 1477	f	r	y	27.79	8	15.32	17.02	depression	
							11.18	13.26	line	2
							6.54	8.41	line	1
155	pre 1300	f	1	y	22.19	8	10.79	12.24	line	2
							7.16	7.43	line	3
							2.47	3.64	line	2
156	pre 1300	e	1	y	31.43	8	12.8	15.65	line	3
							8.88	10.65	line	3
							none	7.02	pits	
160	pre 1300	d	r	y	35.25	5	21.18	22.93	line	1
							16.33	18.61	line	1
							12.44	16.47	line	1
							10.74	13.67	line	1
							9.15	11.24	line	1
165	post 1477	f	r	y	27.3	7	7.35	10.36	depression	
166	pre 1300	c	r	n	34.08	1	none	none		
167	pre 1300	e	1	y	32.87	6	14.73	17.22	line	1
							10.83	13.13	line	1
							8.36	7.85	depression	
168	pre 1300	e	1	y	31.24	8	none	13.54	pit	
169	pre 1300	c	r				none	none		
172	pre 1300	f	r	y	28.17	8	18.61	21.93	depression	
							10.66	15.98	pits	
173	pre 1300	f	r	y	23.17	8	11.56	14.23	depression	
							6.9	7.97	line	2
							none	1.29	pit	

Svalbarð Third Molars

Sample No.	Date	age group	L / R	Crown complete?	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
1	pre 1300	F	R	Y	25.83	10	3.91	5.54	8.87	Depression	
6	pre 1300	f	r	y	29.16	8	none	none	none		
20	pre 1300	f	l	y	30.7	9	8.62	10.94	none	line	
22	post 1477	d	r	n	30.9	1	none	none	none		
26	post 1477	f	l	y	37.71	7	23.75	26.16	24.6	line	1
							18.85	21.53	20.46	line	1
							12.72	14.86	15.57	line	1
							9.62	10.35	10.31	line	1
39	pre 1300	e	l	y	37.1	2	none	none	none		
41	pre 1300	f	r	y	36.7	6	none	13.86	none	pits	
42	post 1477	f	r	y	32.26	8	10.99	12.64	13.56	line	2
							7.56	8.42	8.54	line	4
43	pre 1300	e/f	r	y	39.58	2	none	none	none		
44	pre 1300	e	l	y	35.12	3	none	none	none		
52	pre 1300	f	r	y	32.26	8	12.74	14.2	16	line	1
62	pre 1300	d	l	y	40.36	6	8.02	8.67	10.38	line	1
64	pre 1300	f	r	y	38.21	8	11.35	13.23	15.53	line	3
							8.81	10.97	11.45	pits	
69	pre 1300	F	r	y	30.96	9	6.62	7.69	7.08	line	1
69	pre 1300	f	r	y	33.99	8	14.03	17.08	18.52	depression	
							8.56	11.49	12.18	depression	
							3.11	4.69	7.62	line	2
71	pre 1300	e	l	y	36.39	4	6.17	6.61	8.87	depression	
							none	none	6.34	pit	
72	pre 1300	e	r	y	36.88	4	9.1	11.36	none	pit	
81	post 1477	f	r	y	31.58	9	9.83	10.67	13.11	line	
							3.54	3.99	8.1	pits	
							none	none	3.32	Depression	
82	post 1477	f	r	y	33.13	7	14.26	16.14	17.82	line	1
							10.19	11.89	13.72	line	1
							5.27	5.78	9.05	line	1
83	post 1477	d	l	n	18.72	--	none	none	none		
87	pre 1300	d	l	n	32.17		none	none	none		
88	pre 1300	d	l	n	31.8		none	none	none		
92	pre 1300	F	r	y	35.38	7	30.41	none	none	pits	
							13.97	17.49	none	line	1
							11.39	14.28	none	line	2
							6.56	8.36	none	line	2
101	pre 1300	f	r	y	31.85	9	11.58	14.12	15.85	Depression	
							7.32	7.98	10.77	Depression	
							none	none	2.67	line	2
112	post 1477	f	l	y	35.14	8	28.07	30.68	27.29	pits	
							14.82	16.58	none	line	1
							9.78	none	none	line	1
							3.71	3.74	5.57	line	2
115	post 1477	f	r	y	28.45	8	12.09	15.41	17.98	line	1
							9.12	13.94	none	line	1
							none	none	3.89	line	3
120	pre 1300	e	r	y	38.44	3	none	none	none		
123	post 1477	f	r	n	40.77	2	none	none	none		
128	post 1477	f	l	y	29.42	9	19.95	22.87	24.95	line	1
							4.58	5.4	4.59	line	2
							none	2.71	3.18	line	2
134	pre 1300	e	l	y	36.33	2	17.53	18.93	19.79	line	4
137	pre 1300	f	r	y	33.42	9	10.39	13.2	13.83	line	4
							7.77	9.15	10.33	line	3
							4.2	4.95	5.55	line	2
138	pre 1300	F	r	y	35.16	8	15.31	17.91	18.87	--	
							11.75	15.96	17.22	line	1
							8.82	11.34	none	line	1
141	post 1477	e	3	y	39.53	3	9.78	11.69	12.79	line	1
149	post 1477	f	l	y	35.45	9	11.24	none	none	Depression	
151	post 1477	e	l	y	40.76	3	none	none	none		
154	post 1477	f	r	y	37.25	8	none	20.91	19.92	line	2
							11.11	13.35	13.09	line	2
							5.8	8.2	7.69	line	2
155	pre 1300	f	l	y	28.05	7	13.55	14.89	15.81	Depression	
							7.04	6.72	8.31	line	2
							2.74	3.92	5.08	line	2
165	post 1477	f	r	y	34.76	7	none	none	none		
167	pre 1300	e	l	y	38.87	2	16.57	18.24	19.67	Depression	1
168	pre 1300	e	l	n	38.55	2	none	none	none		
172	pre 1300	f	r	y	33.72	9	10.48	12.72	11.96	depression	
173	pre 1300	f	r	y	33.29	8	9.03	13.65	20.19	line	2
							4.98	8.05	13.3	line	2

Steinbogi First Molars

Sample No.	Age group	L / R	Crown complete?	Hight	wear stage	A Cusp hypo	P Cusp hypo	type	severity
77	C	r	y	25.72	8	calculus	calculus		
79	D	l	y	16.79	8	none	none		
81	?	l	y	25.76	6	none	none		
145	E	l	y	11.37	11	none	none		
182	D	l	y	18.21	8	none	none		
101	c	l	y	29.43	6	none	25.35	line	1
						9.67	10.07	line	1
75	F	l	y	15.05	8	none	none		
78	c	l	y	26.27	7	10.32	13.22	line	1
						none	7.47	line	1
80	D/E	L	Y	18.77	8	none	none		
183	F	r	y	10.6	11	none	none		
156	?	l	y	21.66	8	none	none		
104	D	r	y	27.73	7	15.71	16.37	line	1
						13.41	none	line	1
						4.34	5.52	line	1
76	G	r	y	12.69	9	none	none		
100	G	l	y	11.1	9	8.6	9.62	line	1
102	G	r	y	10.7	10	none	none		
146	D	l	y	21.84	8	none	16	line	1
						9.14	10.85	line	1
180	C	r	y	26.82	7	none	none		

Steinbogi Second Molars

Sample No.	Age group	L / R	Crown complete?	Hight	wear stage	A Cusp hypo	P Cusp hypo	type	severity
77	C	r	n	27.55	unerupted	none	none		
79	D	l	y	31.17	7	8.54	10.19	depression	
145	E	l	y	21.07	8	none	0.96	line	1
182	D	l	y	33	7	12.67	none	line	1
						8.09	5.66	ine	1
						3.74	none	line	1
101	c	l	n	27.93	unerupted	none	none		
75	F	l	y	26.39	8	15.76	17.5	line	1
						12.88	15.07	line	1
						9.72	11.01	line	1
						5.52	6.25	depression	
						none	1.38	line	1
78	c	l	n	28.05	unerupted	none	none		
80	D/E	L	Y	32.45	6	22.54	26.26	line	1
						9.43	10.34	depression	
183	F	r	y	25.31	8	13.15	16.89	line	1
						13.31	14.67	line	1
						8.36	10.62	depression	
104	D	r	n	28.12	unerupted	none	none		
76	G	r	y	23.25	8	15.81	none		
						13.01	17.64	line	1
						9.13	12.85	line	1
						1.86	1.5	line	2
100	G	l	y	23.55	8	18.81	21.68	line	1
						15.29	none	pit	
						13.4	none	pit	
						13.31	15.55	line	1
						8.91	10.88	line	1
						4.86	5.96	line	1
						1.78	2.31	line	2
102	G	r	y	20.86	8	1.13	0.79	line	1
180	C	r	n	32.34	1	none	none		

Steinbogi Third Molars

Sample No.	Age group	L / R	Crown complete?	Height	wear stage	A Cusp hypo	M Cusp hypo	P Cusp hypo	type	severity
79	D	l	n	31.5	unerupted	--	--	--	--	--
145	E	l	y	30.36	10	8.69	10.96	11.44	line	1
						3.27	4.9	3.82	line	1
						0.97	1.16	--	line	1
182	D	l	n	37.38	2	--	--	--	--	--
75	F	l	y	32.56	10	13.25	14.84	16.23	line	1
						11.36	12.12	13.13	line	1
						--	7.74	9.37	line	1
						3.85	3.85	4.95	line	1
183	F	r	y	34.84	10	5.44	6.72	9.78	depression	--
181	?	r	y	31.38	10	calculus	calculus	calculus	--	--
157	?	l	y	28.23	10	--	--	--	--	--
100	G	l	y	32.12	10	--	16.95	18.12	line	2
						4.69	6.18	--	line	1
						1.89	--	--	line	1
102	G	r	y	30.29	10	2.67	3.95	6.69	depression	
						--	0.69	1.56	line	1